

FIRE MOSS: AN UNDERSTUDIED PHENOMENON AND POTENTIAL TOOL FOR
POST-FIRE REHABILITATION

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ABSTRACT

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With wildfires increasing in extent and severity in the Southwestern USA, practitioners need new tools to rehabilitate recently burned ecosystems. Fire mosses consist of three species, *Ceratodon purpureus* (Redshank), *Funaria hygrometrica* (Cord moss), and *Bryum argenteum* (Silvergreen moss). Fire mosses can colonize burned landscapes rapidly and aggregate soils but have not been widely studied. This dissertation explores the potential utility of fire moss as a post-fire ecosystem rehabilitation tool. To better understand where and how quickly mosses colonize after fire, we conducted a natural survey of moss colonization and function on 10 severely burned areas in the southwestern USA. We tested 11 landscape scale predictors of fire moss cover and found that it is most strongly influenced by equinox insolation, pre-fire vegetation type, pre-fire soil organic carbon, and time since fire. We also found that, when compared to bare soils, fire mosses increase infiltration by 50% on average and soil stability by more than 100%.

A major step in developing a new plant materials rehabilitation technique is overcoming propagule limitations using *ex situ* cultivation. We cultivated fire moss gametophyte fragments in the greenhouse allowing us to grow vegetative propagules with control over atmospheric, edaphic, and hydrologic conditions. In this experiment, we grew fire mosses using an easily scalable technique and commercially available materials. We found that fire moss achieved high cover in 2 months when grown on organic substrate with constant wicking hydration and a

protective shade covering, but growth was not favored by addition of burned materials. We demonstrated repeated success growing these species in the greenhouse at increased scales and fine-tuned harvesting techniques to increase productivity.

To test this greenhouse grown moss in the field we conducted three sequential experiments using knowledge gained from previous experiments to fine tune fire moss delivery methods. The first two experiments began one week after full containment of a wildfire in a *Pinus ponderosa* forest of Arizona. First, we added disaggregated (passed through a 2mm sieve) moss tissue to burned soil surfaces, which was immediately collected by ants. In response to the unexpected herbivory pressure, we added two preparations designed to reduce predation: moss rolled into pellets using diatomaceous earth and moss ground to a powder. Pelletization increased *Bryum argenteum* cover and the number of distinct moss colonies when compared to untreated control plots, although cover remained low (1%). The third experiment took place in a mixed conifer forest of New Mexico, USA. Sieved moss, pelletized moss, and pelletized moss at a high (5×) application rate were added to a burned forest, four months after full containment. The high pelletized treatment increased cover to 10% after 1.5 years, but treatments largely converged afterward. At both sites, an exceptional drought during the winter of 2017-18 likely dampened moss establishment. Our results indicate that fire mosses are important colonizers after wildfire, which should be considered when making land management decisions and studied further for their utility as a rehabilitation tool.

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Dedicated to my partner,

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PREFACE

This dissertation follows the journal format with an overall introduction (Chapter I), three body chapters structured as manuscripts for publication in peer-reviewed journals, and a management implications chapter formatted as a factsheet to be disseminated via the Joint Fire Science Program. Chapter II is entitled “Post-wildfire moss colonization and soil functional enhancement in forests of the southwestern USA.” This chapter was published in the *International Journal of Wildland Fire* on 19 February 2020. Chapter III is entitled “Improved, scalable techniques to cultivate fire mosses for rehabilitation” and was published in *Restoration Ecology* on 20 May 2019. Chapter IV is entitled “Pelletized inoculation overcomes insect predation and increases greenhouse-grown fire moss establishment in severely burned forests.” This chapter is formatted to be submitted to *Restoration Ecology*. Chapter V is a factsheet to be circulated via the Southwest Fire Science Consortium. Some redundancy is present to conform to both university and journal formatting guideline.

CHAPTER I

Introduction

Wildfire extent and severity have expanded rapidly in the southwestern US due to climate change and elevated fuel densities (Covington & Moore 1994; Keane et al. 2008; Abatzoglou & Williams 2016; Singleton et al. 2018; Mueller et al. 2020). This creates an urgent need for land managers to better understand and rehabilitate severely burned ecosystems, as they are becoming a common landscape feature (Schoennagel et al. 2017). Research has traditionally focused on recovery and rehabilitation of vascular plants, especially overstory trees, because they are desired management targets (Savage & Mast 2005; Floyd et al. 2006; Ouzts et al. 2015; Owen et al. 2017). As our understanding of the postfire environment grows, often overlooked components of intact forest systems such as soil biota have been shown to be foundational to rehabilitation success (Claridge et al. 2009; Korb et al. 2004). One understudied postfire community are the early successional bryophytes, *Ceratodon purpureus* (Hedw.) Brid. (Redshank), *Funaria hygrometrica* Hedw. (Cord moss), and *Bryum argenteum* Hedw. (Silvergreen moss), often referred to as “fire mosses” because they tend to expand in burned areas (Cremer & Mount 1965; Ryömä & Laaka-Lindberg 2005; Silva et al. 2019).

In this dissertation, I examine the potential utility of fire moss as a postfire rehabilitation tool. This research focused on three main objectives with each objective consisting of one dissertation chapter:

Objective 1: Study the natural role of fire moss in ecosystem recovery after wildfire.

Objective 2: Develop and refine an effective technique to grow moss ex-situ.

Objective 3: Test the effectiveness greenhouse grown moss as a bioinoculant after wildfire and integrate with existing restoration techniques to improve success.

To assist in fire mosses' recovery, a better understanding was needed of when and where they occur naturally in the southwestern US. Additionally, quantifying the restoration value of moss colonization was essential for justifying the cost of rehabilitation (Gann et al. 2019). To achieve these goals, I conducted a survey of moss cover and function in recently severely burned areas. Fire mosses have been documented in a wide range of ecosystem types but tend to attain maximum cover within a few years after wildfire (Hoffman 1966; Southorn 1977; Robinson et al. 2000; Hilty et al. 2004; Pisa et al. 2014). This led me to select burned areas between two months and seven years postfire with the goal of capturing both fire moss growth and subsequent decline. All three fire moss species have high rates of spore production (During 1979; Rosentreter 2019), and long distance dispersal via spores (McDaniel & Shaw 2005). Conversely, genetic turnover and intraspecific variation along steep environmental gradients in relatively short distances has been documented in both *B. argenteum* and *F. hygrometrica* (Magdy et al. 2010; Pisa et al. 2013). This suggests that habitat suitability, not propagule limitation, is the dominant filter of fire moss distribution after fire. Using this information to guide my survey, plot selection was stratified by elevation and insolation within each fire to examine the maximum range of environmental diversity and associated moss cover values.

To better understand the potential benefits of fire moss rehabilitation and function provided by natural colonization, a suite of soil erosion resistance and hydrologic function metrics were measured. Using rapid techniques to take functional measurements allowed me to test moss

associated function at a regional spatial extent. The tradeoff for using rapid techniques was that all measurements were taken at the point scale which may not be indicative of larger watershed properties (Moody et al. 2013). As this was an initial test of moss function, a larger scope of inference was chosen to be sure that results were generalizable across different pre-fire forest communities, edaphic conditions, and moss colonization rates. Results from the survey of natural distribution and function are outlined in Chapter II.

Fire mosses are early successional species that only dominate ecosystems for relatively short time periods (Brasell & Mattay 1984; Esposito et al. 1999). This may make it difficult to collect wild moss propagules in large enough quantities for effective rehabilitation. To overcome this issue, growing moss in a greenhouse setting was attempted to create a renewable and easily accessible source of propagules. Due to the ubiquity of spores, as outlined previously, cultivation of moss gametophyte fragments was prioritized with the eventual goal of increasing survivorship and cover using vegetative propagules (Frey & Kürschner 2011).

Three studies have shown partial success in growing fire mosses (Jones & Rosentreter 2006; Gross 2009; Ives 2016); a combination of these results was used to conduct a greenhouse experiment to grow fire moss propagules. Both Gross (2009) and Jones and Rosentreter (2006) found that *C. purpureus* and *B. argenteum* grew well on topsoil with high organic content sourced from the same location as the mosses. Gross (2009) had difficulty controlling greenhouse climatic conditions using a spray watering technique resulting in death of both species. Jones and Rosentreter (2006) had more success using a growth chamber with lower temperatures and very high relative humidity. Ives (2016) used a wick-from-below watering

method with a sand substrate, amended with ash, selected for its wicking properties (Doherty et al. 2015). This system did not consistently induce sufficient moss growth to be a viable production method (Ives 2016). I tested a variety of substrates and soil amendment combinations with high amounts of organic matter. Materials that could be sourced commercially were used to streamline scaling of production. These techniques were combined with the wicking hydration method, the results of which are outlined in Chapter III.

Biological Soil Crusts (biocrusts) are a diverse set of organisms consisting of cyanobacteria, lichens, and mosses that live on and within the soil and can be dominant components of dryland ecosystems. Fire mosses are a subset of biocrusts with only the moss component, allowing for general comparisons between certain research findings. Current biocrust rehabilitation success is limited by persistence of both greenhouse-grown and wild-collected propagules in the field (Antoninka et al. 2018; Young et al. 2019). Likely barriers such as actively eroding soils or resource limitations were outlined by Bowker (2007) and are common occurrences in recently burned environments (Certini 2005; Shakesby & Doerr 2006).

Fire moss inoculation trials were conducted on two recently burned forests near Flagstaff, AZ and Valles Caldera National Preserve, NM to provide contrasts between sites and increase the potential for success. Recently, biocrust field establishment in drylands has been driven by stabilization techniques of organic jute cloth and soil tackifiers (Condon & Pyke 2016; Fick et al. 2019; Slate et al. 2019), but success can be limited to specific climatic and edaphic conditions (Faist et al. 2019). One detriment to these techniques is increased cost and difficulty of scaling so I initially opted to add dried greenhouse grown moss on its own. In the first experiment, ant

predation of mosses was extremely high, underscoring a previously unrecognized barrier to biocrust recovery and expansion. Subsequent treatments were implemented to reduce that predation and increase establishment while maintaining scalability of treatments. These efforts are detailed in Chapter IV.

Chapters II through IV show that fire moss is an important part of postfire recovery and outline a framework for rehabilitation. To increase the accessibility of this research to the ecological restoration and land management communities, results have been summarized in a factsheet in Chapter V. This includes a description of where and when fire moss is most likely to be found post-fire and photos of early stages of colonization which will be valuable to managers when monitoring postfire recovery. Additionally, we outline the most successful techniques for cultivation and field inoculation of fire mosses.

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CHAPTER II

Post-wildfire moss colonization and soil functional enhancement

in forests of the southwestern USA

Abstract

Fire mosses, including *Ceratodon purpureus*, *Funaria hygrometrica*, and *Bryum argenteum*, can achieve high cover within months to years after high severity fire, but do so heterogeneously across space and time. We conducted a survey of moss cover and erosion-related functions after ten wildfires in *Pinus ponderosa* and mixed-conifer forests of the southwestern USA. We sampled 65 plots in high severity patches, stratifying by elevation and insolation over each fire. Using three landscape-scale predictor variables and one temporal predictor, we explained 37% of the variance in fire moss cover using a random forest model. The predictors in order of importance were: equinox insolation (sunlight/day), pre-fire vegetation type, pre-fire soil organic carbon, and time since fire. Within each plot we examined differences between bare and moss-covered soil surface microsites and found moss-covered microsites had a mean increase of: 56% water infiltration, 105% shear strength, 159% compressive strength, and 192% aggregate stability. We tested a suite of nutrients, finding 35% less manganese in the moss-covered soil. This research demonstrates that post-fire colonization by moss is predictable and that colonization improves soil surface erosion resistance and hydrological function, with implications for managing severely burned landscapes.

Additional keywords

Bryum argenteum; *Ceratodon purpureus*; *Funaria hygrometrica*; ponderosa pine forest; mixed-conifer forest; soil erosion; post-fire

Brief summary

Fire mosses are early successional species that can colonize severely-burned landscapes. We conducted a survey of ten wildfires in the southwestern USA. Fire moss cover increased in shaded north-facing hillslopes in relatively wet locations. When compared to the bare soil surface, fire mosses reduced erosion and enhanced water infiltration.

Introduction

Fire extent and severity have been increasing in the southwestern United States (USA) due to climate change and elevated fuel densities (Abatzoglou & Williams 2016; Keane et al. 2008; Singleton et al. 2018). This creates an urgent need to better understand and adapt to the severely burned environment as it is quickly becoming a common landscape feature (Schoennagel et al. 2017). To assist land managers in understanding the severely-burned environment, researchers have studied natural post-fire recovery of vascular plants in detail (Savage & Mast 2005; Kuenzi et al. 2008; Roccaforte et al. 2012; Owen et al. 2017). Non-vascular plants can be important post-fire colonizers as well. The recolonization of the soil surface by the early successional mosses, *Ceratodon purpureus* (Hedw.) Brid. (Redshank), *Funaria hygrometrica* Hedw. (Cord moss), and *Bryum argenteum* Hedw. (Silvergreen moss), collectively known as fire mosses, has not been studied in the southwestern USA and only sparingly elsewhere (Brasell & Mattay 1984; Hoffman 1966; Southorn 1977; Hilty et al. 2004). These globally distributed species can achieve high cover in recently-burned environments (Brasell & Mattay 1984).

Mosses have many functional traits that allow them to enhance ecosystem recovery after disturbances. For example, they have been documented to increase infiltration, aggregate soil surfaces, and reduce erosion (Chamizo et al. 2012; Bu et al. 2015; Seitz et al. 2017; Silva et al. 2019). Fire mosses have both long- and short-distance dispersal methods, allowing them to quickly colonize and attain high cover in large severely-burned patches (Frey & Kürschner 2011; McDaniel & Shaw 2005; Jones & Rosentreter 2006; Ryömä & Laaka-Lindberg 2005). Fire mosses, like other biocrusts, grow in a thin layer at the soil surface, stabilizing soil to a degree disproportionate to their biomass (Jones et al. 1997). Fire mosses are desiccation tolerant, meaning they can dry without dying, allowing them to survive long periods of drought (Proctor et al. 2007). To our knowledge, no studies have focused on the natural role of mosses in post-fire recovery in the southwestern USA. Therefore, we conducted a survey of natural moss colonization and function in recent high-severity burn patches in conifer forests with two main objectives. First, understanding the temporal- and landscape-scale drivers of moss cover will assist managers in predicting when and where fire moss could colonize. Second, exploring the moss-associated benefits in erosion resistance, hydrological function, and soil nutrients will allow managers to better understand the potential value of preserving fire moss cover after wildfire.

We hypothesized that fire moss cover would reach maximum cover within two years following fire, as documented in the northwestern USA and Tasmania, Australia (Hoffman 1966; Brasell & Mattay 1984). To test this, we sampled fires at a range of elapsed times between fire and sampling (hereafter time since fire), from two months to seven years. We hypothesized that mosses would prefer higher elevation sites on relatively shady hillslopes as seen in the

northwestern USA (Hoffman 1966; Hilty et al. 2004; Durham et al. 2018). To test this, we selected plots that occurred in *P. ponderosa* and mixed-conifer forests at a range of elevations and winter solstice insolation positions (the amount of sunlight received on the winter solstice) within those ecosystem types, crossing factors to the maximum degree possible.

To test fire mosses' contribution to post-fire ecosystem erosion resistance and hydrological function, we compared bare mineral soil to moss-covered soil surfaces (hereafter bare vs moss) using a within-plot paired microsite technique. Biocrusts in Australian drylands have shown an affinity for trapping dust, we hypothesized that moss would trap fugitive ash and its associated nutrients when compared to adjacent bare soils (Mallen-Cooper & Eldridge 2016; Pereira et al. 2014). Alternatively, mosses could preferentially uptake limiting nutrients and could decrease some nutrient concentrations. Because of mosses' ability to aggregate disturbed soil (Seitz et al. 2017; Xiao et al. 2015; Silva et al. 2019), we hypothesized fire moss would increase both erosion resistance and infiltration when compared with bare soil; we used four measurements to test this hypothesis.

Methods

Fire and Plot Selection

We selected three regions within the southwestern USA: Flagstaff in northern Arizona, the White Mountains in eastern Arizona, and the Jemez Mountains in northern New Mexico. Each region experienced multiple severe fires in the recent past. Within these regions, we selected fires encompassing a range of times since fire (**Table 2.1**). During the summers of 2016 and 2017 we sampled a total of ten fires.

Within each fire, we selected plots in high-severity burned areas as determined by Monitoring Trends in Burn Severity (MTBS). High severity was based on the relativized differenced normalized burn ratio (RdNBR), a vegetation burn severity index that is standardized for between-fire comparisons (Eidenshink et al. 2007). We used RdNBR pixels > 643 , a threshold specific to the southwestern USA (Singleton et al. 2018). If MTBS products had not yet been created, we used the high soil burn severity class created by Burned Area Emergency Response assessment teams (Hudak et al. 2004). Because soil burn severity and RdNBR can be poorly correlated (Safford et al. 2008), we validated high canopy-burn severity in the field by observing tree mortality of $>90\%$. We limited our scope of inference to high burn severity areas because of the increased runoff and erosion potential from that burn class (Scott et al. 2009; Shakesby & Doerr 2006). To reduce the possibility of sampling small patches of high fire severity, we cropped the perimeter of each patch by 30 m or one pixel, thus deleting any patch two pixels wide or less. We selected a subset of pixels 30 to 230 m from accessible roads to minimize time spent walking to plots.

The remaining severely-burned areas within each fire were stratified by elevation and winter solstice insolation to maximize the environmental diversity of plots sampled. A 10 m digital elevation model (DEM) was used for all calculations in this stratification (Gesch 2007). We first excluded areas with slopes $> 85\%$ for safety, then extracted elevation from remaining pixels. To derive insolation, we calculated direct radiation modified by terrain and total diffuse radiation at each hour of the day, but excluded the minimal effects of sky view and changes in relative humidity and temperature throughout the day (Corripio 2003). To stratify by insolation and

elevation we used cluster analysis, an analytical tool used to conduct stratified sampling of multivariate environmental data (Hargrove & Hoffman 2004). We applied the computationally efficient k-means algorithm from the *Stats R Package* (Hartigan & Wong 1979). The number of clusters (k) per fire was selected arbitrarily depending on its size, environmental diversity, and if we had previously sampled a similar time since fire, resulting in 3 to 15 clusters per fire (**Table 2.1**). To capture the full range of environmental diversity within fires, we first selected plots at the extreme values of elevation and insolation, then one plot location was selected at random from within each cluster.

We relocated four plots by up to 100 m to target specific topographic conditions or to avoid disturbed areas such as roads. Plots consisted of two 20 m transects, 20 m apart, along two parallel contours. At three plots, topography did not allow for 20 m of continuous hillslope so transects were moved closer together. We took GPS coordinates at the four corners created by the transect end points, and averaged them to obtain plot locations for GIS analysis. Along each transect, we measured percent fire moss cover using a line intercept method with a resolution of 1.5 cm (Canfield 1941). If moss was not found on a transect, we used a five-minute timed search within 5 m of the transects to determine presence or absence, allowing us to distinguish true absences from low abundances.

Paired microsite measurements

To test fire mosses' contribution to erosion resistance and hydrological functional we measured paired bare vs moss microsites and collected paired soil samples for laboratory analysis (Bowker et al. 2006). This only occurred if moss cover was high enough, defined as roughly 400 cm² of

moss in at least six patches per plot within a 5 m buffer around the transects. Microsites were spaced 10 cm to 2 m apart, and microsite pairs were dispersed throughout the plot to the degree that moss cover allowed. At each plot we measured: infiltration rates at three bare vs moss pairs using a Mini Disc Infiltrometer™, Meter Environment, Pullman, Washington, USA (Robichaud et al. 2008); soil shear strength at six pairs using a Torvane™ shear vane, Durham Geo-Enterprises, Mukilteo, Washington, USA (Zimbone et al. 1996); soil compressive strength at six pairs using a handheld penetrometer, QA Supplies, Norfolk, Virginia, USA (Zimbone et al. 1996); and soil aggregate stability at 12 pairs using a soil aggregate stability test kit (Herrick et al. 2001). To ensure a uniform hydraulic connection between the infiltrometer and the soil surface, we drove a 5 cm diameter metal ring into the soil 3 cm deep and added a thin layer of sand until the soil or moss was entirely covered. The infiltrometer was then held in place inside the ring using a stand, without applying any downward pressure. Microsites for Torvane™ and penetrometer measurements were wetted to field capacity with a spray bottle before taking measurements. At <10% of microsites, the functional measurement observed was below the detection limit of the instrument, so we assumed function was half of the lowest measurement increment of that instrument. To the degree possible, we sampled plots when the soil surface was dry to increase consistency of moss cover measurements between plots and soil moisture between moss and bare microsites.

We received permission to collect soil samples from all burned areas except two (the Wallow and San Juan Fires). Soil sampling consisted of five to ten subsamples, depending on size and number of moss patches available, directly under live moss tissue to a depth of 1.5 cm, and on the bare mineral soil microsites to a depth of 1.5 cm. We removed moss fragments from samples

before analysis. In the lab, soil samples were sieved in a 2 mm sieve and analyzed for pH, organic carbon, total nitrogen, available phosphate, and a suite of available cations and trace metals, following the Forest Inventory Analysis Protocol (Amacher et al. 2003). We measured pH using a glass electrode immersed in a saturated paste of 10 mg soil mixed with a .01 M CaCl₂ solution and allowed to stand for 30 minutes. Carbon and Nitrogen samples were ground and analyzed using a 4010 Elemental Combustion System (Costech Analytical Technologies Inc. Valencia, CA). Phosphate was extracted using the Olsen (pH > 6) and Bray (pH ≤ 6) methods and analyzed using a Lachat Instruments QuikChem 8500 series Flow Injection Analyzer (Lachat Instruments, Loveland, Colorado, USA). Water soluble cations and metals were extracted using a 1M NH₄Cl solution. We used an argon gas carrier and analyzed samples on a Thermo Scientific™ iCAP™ 7000 Series ICP-OES (Inductively Coupled Plasma-Optical Emission Spectrometry) or mass spectrometry (ICP-MS), using Qtegra™ ISDS™ Software. Cations and metals consisted of calcium, magnesium, potassium, sodium, sulfur, aluminum, and manganese. Additionally, we measured total iron, copper, zinc, nickel, cadmium, and lead but their concentrations were below detection levels.

Landscape predictors of fire moss cover

To elucidate landscape-scale drivers of fire moss cover, we selected variables with continuous coverage within our study system. We selected 11 candidate predictors in six broad categories: temporal, topographic, solar, climatic, vegetative, and edaphic (**Table 2.2**). Our first predictor was time since fire (years). Topographic predictors of elevation (m) and slope (degrees) were extracted using the same 10 m resolution DEM as in the plot selection methods. Topographic Wetness Index (unitless) was calculated from the DEM using SAGA GIS (Conrad et al. 2015).

Two solar predictors of insolation (MJ m^{-2}) were calculated as described in the plot selection section of this manuscript. We used insolation on the equinox summed over the entire day and at 0900 hours. Equinox insolation was found to be a superior predictor to winter solstice insolation because some locations receive no direct sunlight in steep terrain during winter. Equinox insolation at 0900 hours was used to differentiate slopes that receive morning vs evening sun, which is a potential driver of hydration period length during daylight. PRISM climate normals (1981-2010) of yearly precipitation (mm) at a resolution of 800 m were extracted (Daly et al. 2008). Edaphic variables of pre-fire soil organic carbon (%) and pH, at 0 cm depth, were extracted from Soil Grids at a resolution of 100 m (mapping accuracies pseudo $R^2 = 0.41$ and 0.68 , respectively, Ramcharan *et al.* 2018). An edaphic variable of geologic map unit containing 10 categories was extracted from the State Geologic Map Compilation geodatabase (Horton et al. 2017). Categories were combined into five major classes: Alluvium, Andesite, Basalt, Sedimentary, and Tuff, to reduce the risk of spurious results from many categories (Hastie et al. 2017). We used the pre-fire 2012 LANDFIRE existing vegetation type layer at a resolution of 30 m to determine vegetative effects on moss growth (Ryan & Opperman 2013). Our dataset contained three categories: Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland (hereafter mesic mixed-conifer), Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland (hereafter dry-mesic mixed-conifer), and Southern Rocky Mountain Ponderosa Pine Woodland (hereafter ponderosa pine).

Modeling moss cover

We modeled moss cover in R version 3.5.1 (R Core Team 2019) using the random forest machine learning algorithm (Breiman 2001) in the randomForest package (Liaw & Wiener

2002). We first created a random forest model with all candidate predictors to assess variable importance. Then we optimized this model using a variable selection technique, and finally reran the optimized model using the selected predictor variables. Random forest is a nonparametric machine learning algorithm implemented by taking bootstrap samples of the data and fitting decision trees to each replicate. At each decision tree node, the variable that minimized regression error was selected from a random subset of predictors. We used the total number of predictors divided by three for each node predictor subset. Nodes were split until no further reduction in error was achieved. Observations not selected in the bootstrapping process, termed “out of bag” (OOB), were used to compute the mean squared regression error for each tree. We then averaged the errors and took the square root to calculate the model root mean squared error (RMSE). Random forest variable importance results can be sensitive to changes in random seed if the number of trees grown is too small (Strobl et al. 2008). We ran models multiple times using different random seeds and looked for rank changes in permutational variable importance of predictors. We found variable importance rank stability for the most important variables to be 5000 trees per model and three predictors per node subset.

When using random forests, selecting the most important variables not only increases model interpretability and parsimony, it can also improve model performance (Evans et al. 2010). The two major reasons for this improvement are: only good predictors are selected during the node splitting phase of the algorithm (Hastie et al. 2017), and as spurious variables are removed from the model, trees tend to have fewer nodes, thus decreasing the noise of each tree and increasing the signal to noise ratio of the forest (Evans et al. 2010). We used the VSURF package to implement a variable selection approach (Genuer et al. 2013). The VSURF package ranks

predictor variable importance and then uses a stepwise forward approach to introduce variables into the model. Predictors are only added if the decrease in OOB error is greater than a threshold value of the average variation introduced by adding permuted variables (Genuer et al. 2013). After this selection technique we reran the randomForest package to create an optimized model using four predictor variables, with 500 trees, and one selected variable per node.

Visualizing drivers of moss cover

Using the optimized model, we implemented a similar but improved version of partial dependence called Accumulated Local Effects (ALE) to create bivariate plots of how each predictor affected moss cover (Apley & Zhu 2019; Friedman 2001). ALE plots use a moving window to calculate how the predictor affects the response for data instances within that window. The advantage of ALE plots over partial dependence is their robustness when predictor variables are correlated (Apley & Zhu 2019). This technique was implemented using the IML package (Molnar *et al.* 2018). We included the raw data within each bivariate plot to increase interpretability.

Using the optimized model, we made a map of model-predicted moss cover, and the three best predictors in severely-burned conifer forests of the Slide Fire, two years post-fire. One limitation to bivariate plots is that they do not allow us to visualize interactions between predictor variables. Interactions, however, can be visualized on a map.

Paired microsite data

For each hydrological and erosion measurement, at each microsite pair, we calculated the percent change from bare to moss-covered soil. We then calculated a plot level mean for each measurement type. Because soil samples were composited before analysis, plot level means of soil properties were measured directly. To calculate study-wide summary statistics of hydrological and erosion measurements and soil nutrients we bootstrapped 95% confidence intervals for the mean with 10000 replicates using the boot package (Canty 2002).

Results

Modeling moss cover

Moss cover ranged from 0 to 72.9% with a mean of 11.2% and a median of 3.5% (**Fig. 2.1**). Our initial model of moss cover had an OOB RMSE of 13.2 and a pseudo R^2 of 0.30. We used permutational variable importance, which is defined as the change in the model accuracy when that variable is permuted and the model rerun. It is robust to unstandardized predictor variable scales (Hastie et al. 2017). The most important variables were equinox insolation (57.1), pre-fire soil carbon (20.2), and (13.9, **Fig. 2.2a**). Time since fire, elevation, and precipitation, were the next most important variables. Their importance rank order changed with different random seeds and ranged from 12.0-11.6 (**Fig. 2.2a**). Equinox insolation at 0900, geologic map unit, slope, topographic wetness index, and pH were poor predictors of moss cover (Fig. 2a).

Four variables were selected for the optimized model: equinox insolation, pre-fire vegetation type, pre-fire soil organic carbon, and time since fire. This model performed substantially better than the initial model with an OOB RMSE of 12.5 and a pseudo R^2 of 0.37. The most important

predictor was equinox insolation (62.5), followed by pre-fire vegetation type (40.8), pre-fire soil carbon (31.5), and time since fire (20.1, **Fig. 2.2b**). The rank order importance of these predictors was consistent across six model runs with different random seeds.

Visualizing drivers of moss cover

In the ALE plots, moss cover had a relatively linear, inverse relationship with equinox insolation (**Fig. 2.3a**). Pre-fire vegetation type had three levels: Moss cover was highest in mesic mixed-conifer forests with a mean of 17.0%, followed by ponderosa pine forests with a mean of 10.3%; dry-mesic mixed-conifer forests had the lowest moss cover at 6.9% (**Fig. 2.3b**). Moss cover was positively related to soil organic carbon with high moss cover found within a range of organic carbon values from 22-33% (**Fig. 2.3c**). Time since fire was the final predictor included in our optimized model. Initially, moss cover was low after fire but increased to a maximum at two years and then dissipated as time since fire increased to greater than five years (**Fig. 2.3d**).

Predicted moss cover on the Slide Fire ranged from 0% to 44% and was heterogeneous across the landscape (**Fig. 2.4b**). Most of the area burned was south-facing with insolation levels above 20 MJ m⁻² in the ponderosa pine ecosystem type (**Fig. 2.4b-c**). This resulted in <10% moss cover across most of the fire with localized patches of high cover in steeper north-facing slopes (**Fig. 2.4b-c**). This map is useful for visualizing drivers of moss cover across the landscape. However, given our intermediate model performance metrics (RMSE =12.5) and lack of independent cross validation (Evans et al. 2010) we would expect differences between our prediction and actual cover values.

Paired microsite data

We examined nutrient differences on bare vs moss microsites at 29 plots in Flagstaff and the Jemez mountains. Only pH, potassium (K), and manganese (Mn) differed from bare to moss microsites (**Fig. 2.5**). We found that pH increased by 3.6% from a mean of 6.25 on bare to 6.45 on moss sites, K increased by 14.0% from a mean of 922.0 (mg kg⁻¹ soil) on bare to 984.1 (mg kg⁻¹) on moss sites, and Mn concentrations decreased by 34.7% from bare to moss microsites.

Moss was superior to the bare soil surface for all metrics of erosion resistance and hydrological function (**Fig. 2.6**). Forty-eight plots had enough moss to measure infiltration and 50 had enough to measure shear strength, compressive strength, and aggregate stability. The percent difference from bare to moss microsites for each measurement are as follows. Percent change in infiltration ranged from -46% to 280.4% with a mean of 54.9% and a median of 48.2%. Shear strength ranged from -30.1% to 645% with a mean of 105.9% and a median of 74.3%. Compressive strength ranged from -23.7% to 578.6% with a mean of 162.2% and a median of 97.6%. Finally, aggregate stability ranged from 0% to 500% with a mean of 195.2% and a median of 166.3%. None of the bootstrapped 95% confidence intervals for the mean overlapped zero (**Fig. 2.6**).

Discussion

Landscape scale controls of fire mosses

Consistent with our hypothesis, moss colonization was negatively related to equinox insolation; that is, shady north-facing slopes had higher cover. The duration of continuous hydration, or conversely the speed of desiccation, often controls moss productivity (Proctor 1990; Proctor et al. 2007) and south-facing slopes in the northern hemisphere dry mosses more rapidly, limiting

growth. This effect is amplified in severely-burned forests where soil surface temperatures can be 3-7 °C higher than in unburned forests (Montes-Helu et al. 2009). Conversely, mosses are relatively shade-tolerant with a median daily light saturation value across 39 species of 11 MJ m⁻² (Marschall & Proctor 2004). The minimum equinox insolation value for our study was 14 MJ m⁻² so light limitation likely did not occur.

The importance of pre-fire vegetation type was not surprising, as it unites many different climatic and topographic factors into a single variable. Cooler and wetter regions supporting mesic mixed-conifer forests would be expected to enhance moisture retention time in surface soils and mosses, thus increasing growth. More puzzling was the finding of higher moss cover in ponderosa pine forests compared to dry-mesic mixed-conifer forests. This result was influenced by the fact that 10 of the 15 dry-mesic mixed-conifer plots sampled were within the Schultz Fire extent, which had among the lowest moss cover values (**Table 2.1**). We hypothesize that some feature of the Schultz Fire distinguishes it from the other fires in this study. For example, this fire experienced extremely high rates of post-fire erosion (Neary et al. 2012), which could have influenced subsequent moss growth. Alternatively, this fire was among the oldest sampled and it is plausible that our observations missed an earlier peak in biomass (Hoffman 1966; Brasell & Mattay 1984). To determine whether our observations are typical of dry-mesic mixed-conifer forests would require more intensive sampling of this community type.

While it is true that vegetation types differ in surface soil carbon content with high values in mesic mixed-conifer forests, our results suggest that there is predictive value in pre-fire soil carbon that is independent of vegetation type. The positive relationship between moss cover and

pre-fire soil carbon could be attributed to an enhancement of the post-fire soil environment that enhances moss growth. While surveying, we often found within a given plot, fire mosses preferentially colonized soil adjacent to burned coarse woody debris (Ryömä & Laaka-Lindberg 2005). We hypothesize that a similar trend could be occurring at the landscape scale, wherein fire consumes soil carbon to create a substrate that is then preferentially colonized by moss. This hypothesis has been partially tested experimentally with fire mosses growing rapidly on unburned organic substrates in a greenhouse (Grover et al. 2019). However, fire mosses have also been shown to preferentially colonize bare mineral soil after disturbance (Kranabetter et al. 2017; Gross 2009).

The relationship between moss cover and time since fire is relatively noisy because of our within-fire plot stratification. However, there is support for our hypothesis that moss cover increases until two years post-fire and gradually declines after that. This could be because of competition with vascular plants (Lewis et al. 2017) or changes in substrate as recovery occurs (Certini 2005), but we did not test this directly. The first two years post-fire is a typical range of times in which maximum cover is seen in diverse ecosystems throughout the globe (Silva et al. 2019; Esposito et al. 1999; Brasell & Mattay 1984; Hoffman 1966). Our data seem to suggest an abrupt increase from very low cover to peak levels in year 2, but we have reason to suspect that our dataset may underestimate moss cover before 2 years post-fire. During our sampling period of 2016 and 2017 there was a lack of predominantly high severity wildfires in the southwestern USA. Instead, we sampled fires managed for ecosystem benefit that occurred in relatively flat topography, in ponderosa pine ecosystems, and did not create large patches of high burn severity. This is a limitation of the space-for-time substitution method. Early growth of mosses (< 2 years

post-fire) merits further investigation with repeated monitoring of the same locations, beginning directly after wildfire within a diverse set of forest types.

The map of the 2014 Slide Fire shows the drivers of moss cover in complex terrain (**Fig. 2.4**).

One can see the main effect of each variable, but the real utility of this map is examining how variables relate to each other. For example, we can see synergistic interactions on the eastern portion of the north rim of the canyon. Here, the convergence of low equinox insolation and high pre-fire soil organic carbon corresponds to patches of very high predicted moss cover.

Conversely, we can see instances where some favorable conditions are met, but not others, for example on the eastern portion of the south rim of the canyon. Here, there exists a comparable amount of low equinox isolation habitat as on the north rim, but the patches of high predicted moss cover are fewer and smaller. Possibly this is because the south rim of the canyon has a higher proportion of dry-mesic mixed-conifer forest rather than ponderosa pine forest, as well as lower pre-fire soil organic carbon. One relationship that is not easily visualized with this map is how elevational patterns could be driving pre-fire vegetation independently of equinox insolation (Merriam 1890). This pattern is evident in the San Juan and Wallow Fires as they spanned a wide range of elevations and equinox insolation. This contributes to the evidence that pre-fire vegetation type is a coarse but adequate predictor of elevation and climate.

Moss-mediated alterations of soil nutrients

High-severity fires affect soil nutrient concentrations and availability, with consequences for plants, especially at the soil surface (Certini 2005). With ash deposition, increases in pH and base cations are to be expected (Pereira et al. 2014). The increase in pH and K from bare to moss-

covered microsites is consistent with scenarios in which mosses either preferentially colonize ash-covered soil or trap mobile ash, as dust is trapped by mosses in other environments (Mallen-Cooper & Eldridge 2016). The decrease in Mn under mosses could be attributed to moss depletion of Mn in the soil directly under it. Alternatively, Mn in mobile ash may be entrained in the moss cushion, and physically prevented from entering the soil beneath.

Effect of moss on erosion resistance and infiltration

Flooding and erosion are among the costliest outcomes of high-severity fire; thus promoting biota that enhance ecosystem recovery is commonly a management priority. Our results show a doubling in erosion resistance on average and 1.5 times more infiltration which point to the potential for mosses to reduce erosion and runoff after fire. It is generally accepted that a high surface cover of bare soil is a strong predictor of increased hillslope runoff and erosion (Scott et al. 2009). Our results indicate that fire moss could help remedy erosion and hydrological disfunction and should be accounted for when considering postfire management strategies.

Similar studies support our results that greater moss coverage leads to less erosion (Silva et al. 2019; Xiao et al. 2015; Bu et al. 2015; Seitz et al. 2017). Mosses may dissipate the force of falling raindrops or protect against the erosive force of runoff. A key caveat to our results is the point-scale at which these measurements were taken. Post-fire erosion is largely driven by the formation of rills and gullies which our experimental design did not take into account (Moody et al. 2013). Bu *et al.* (2015) tested point scale soil shear strength measurements, which were predictive of erosion in 4 x 2 m runoff plots. Thus, our measurements likely scale up, but overall the literature is lacking data on the effect of mosses on erosion at hillslope and watershed scales.

Many of the same studies that support our finding of moss-enhanced erosion resistance did not find enhanced infiltration or reduced runoff on moss-covered soils (Bu et al. 2015; Silva et al. 2019; Xiao et al. 2015). This discrepancy is likely due to differences between tension infiltrometer and runoff plot methodology. Experimental manipulations focused on moss-covered burned soils reaction to both sheet flow and channelized flow would be useful to understand function at increased scales (Pannkuk & Robichaud 2003).

Conclusions

This research provides a better understanding of the distribution, and potential limitations to growth of a previously understudied early successional post-fire community. We found that fire mosses generally prefer shady hillslopes in mesic forests with high pre-fire soil organic carbon and reach maximum cover 2 years post-fire. Furthermore, we provide evidence that post-fire moss growth is likely to positively affect erosional and hydrological function. This moss-associated increase in function suggests that managers should actively encourage moss cover and avoid disturbances that potentially inhibit it after fire. This study creates a basis for testing the effects of post-fire management techniques such as Burned Area Emergency Response treatments or salvage logging on fire moss colonization. The global distributions of fire mosses mean that they could be an important component of the post-fire community in other regions and ecosystems that experience high-severity fire and should continue to be studied both for their ecological significance and potential utility in post-fire rehabilitation.

Authors' Contributions

HG designed, conducted the survey and the analyses, and wrote the manuscript. MB, PF secured the funding, advised in the design and analysis, edited the manuscript. KD designed the sampling stratification, made the map, edited the manuscript. CS, AA advised in the design, provided funding, edited the manuscript.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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Table 2.1. Fires sampled. TSF, time in decimal years between fire start date and sampling; moss mover = mean and (range) of moss cover plots within fire.

Fire	Region	Start Date	TSF (Years)	Size (Ha)	Plots	Moss Cover (%)
Schultz	Flagstaff, AZ	20100620	6.0, 7.0	5,648	12	1.3 (0-10.1)
Slide	Flagstaff, AZ	20140620	2.0, 3.0	8,590	10	14.1 (.6-46.1)
Camillo	Flagstaff, AZ	20150614	2	9,977	3	0.8 (0-2.35)
Pivot Rock	Flagstaff, AZ	20160518	1.1	2,434	4	0.02 (0.02-0.02)
Jack	Flagstaff, AZ	20160529	.22, 1.1	24,709	4	0 (0-0.025)
Las Conchas	Jemez Mtns, NM	20110626	6	61,057	3	13.2 (3.2-22.0)
Thompson Ridge	Jemez Mtns, NM	20130531	4	9,186	4	22.7 (.2-52.3)
Diego	Jemez Mtns, NM	20140625	3.1	1,467	3	5.7 (0-16.8)
Wallow	White Mtns, AZ	20110529	5.1	228,107	15	14.6 (1-36.3)
San Juan	White Mtns, AZ	20140626	2	2,975	7	30.9 (1.4-72.9)

Table 2.2. Predictors used for modeling moss cover at the landscape scale.

Predictor	Resolution	Units	Mean	Median	Range
Time since fire	N/A	Years	1315.32	1129	79-2559
Elevation	10m	m	2388.87	2397.1	1569.93-3005.86
Slope	10m	degrees	15.53	15.1	1.01-41.93
Topographic wetness index	10m	unitless	5.99	5.82	4.02-11.20
Equinox insolation	10m	MJ m ⁻²	22.94	23.95	14.51-27.49
Equinox insolation 0900 hours	10m	MJ m ⁻²	0.94	0.95	0.33-1.38
Precipitation	800m	mm	687.81	683.41	538.21-887.40
Pre-fire soil carbon	100m	%	24.34	25.6	13.7-32.9
pH	100m	Unitless	6.15	6.2	5.60-6.60
Geologic map unit	polygon	N/A	N/A	N/A	N/A
Pre-fire vegetation type	30m	N/A	N/A	N/A	N/A



Figure 2.1. High fire moss cover 2 years after fire: (a) 2014 San Juan Fire: and (b) 2014 Slide Fire. Photo credit: Henry Grover.

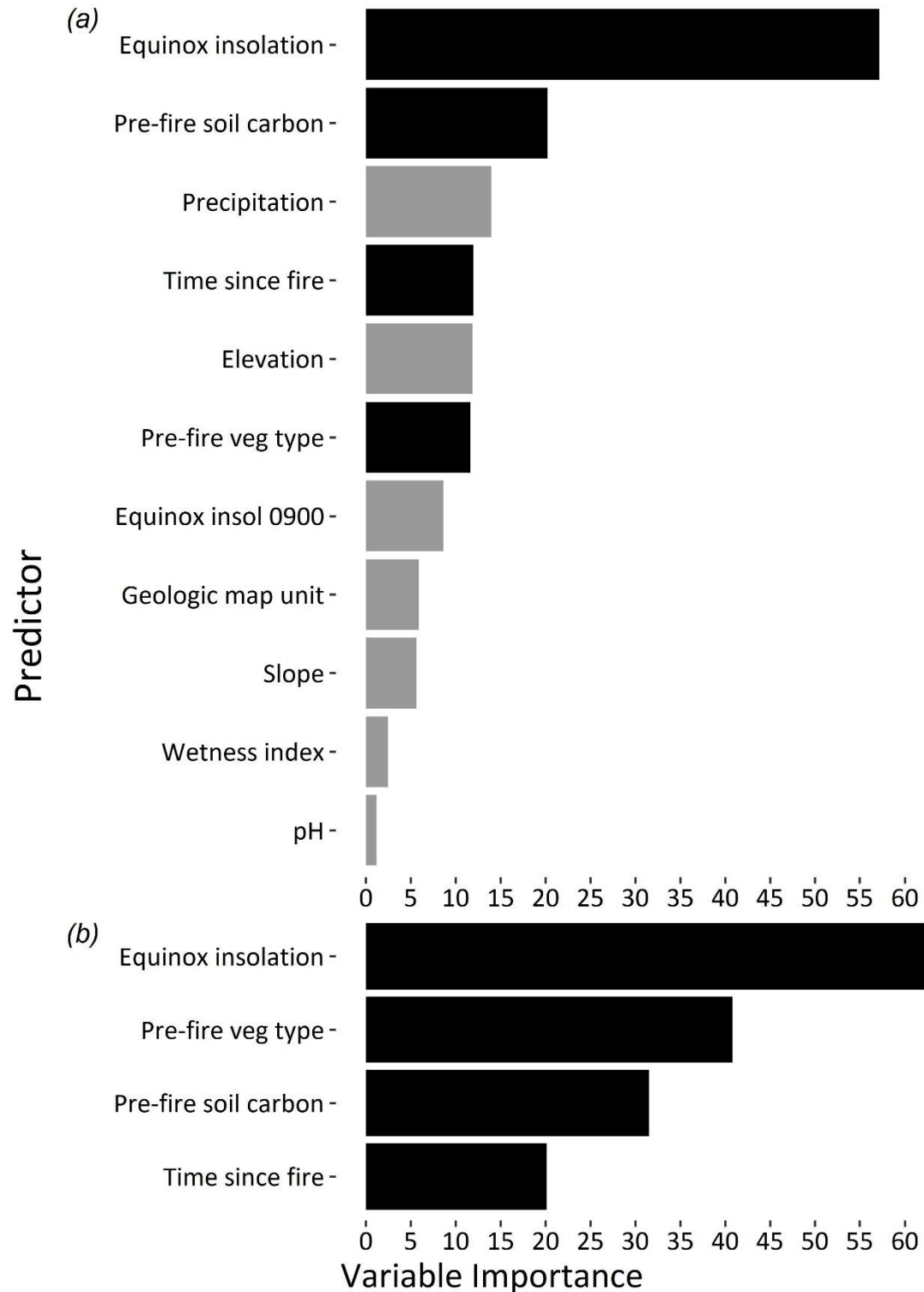


Figure 2.2. Variable importance for (a) the *a priori* model, defined as the percent increase in RMSE when the variable of interest is permuted (RMSE = 13.2, pseudo R^2 = .30), and (b) Variable importance scores for optimized model (RMSE= 12.5 , pseudo R^2 = .37)

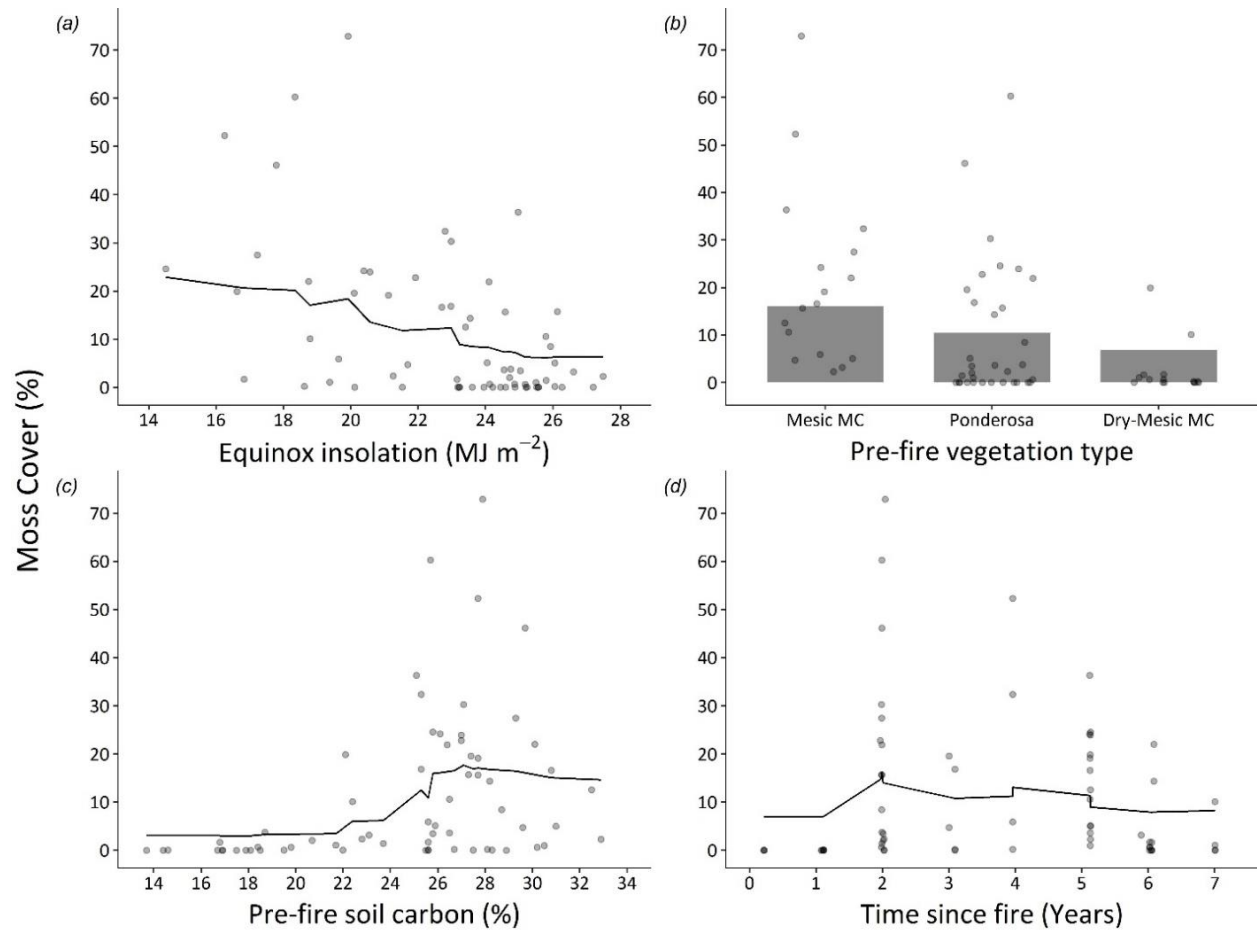


Figure 2.3. Bivariate plots of predictors in optimized model in order of importance: (a) equinox insolation, (b) pre-fire vegetation type (MC = mixed-conifer), (c) pre-fire soil surface organic carbon, and (d) time since fire. Predictions (lines and bars) are random forest accumulated local effects, a visualization of how each predictor variable affects the response when other main effects and interactions are accounted for. Points are plot values ($n = 65$). Black dots denote superimposed data points, in panel (b) points have been separated for easier visualization.

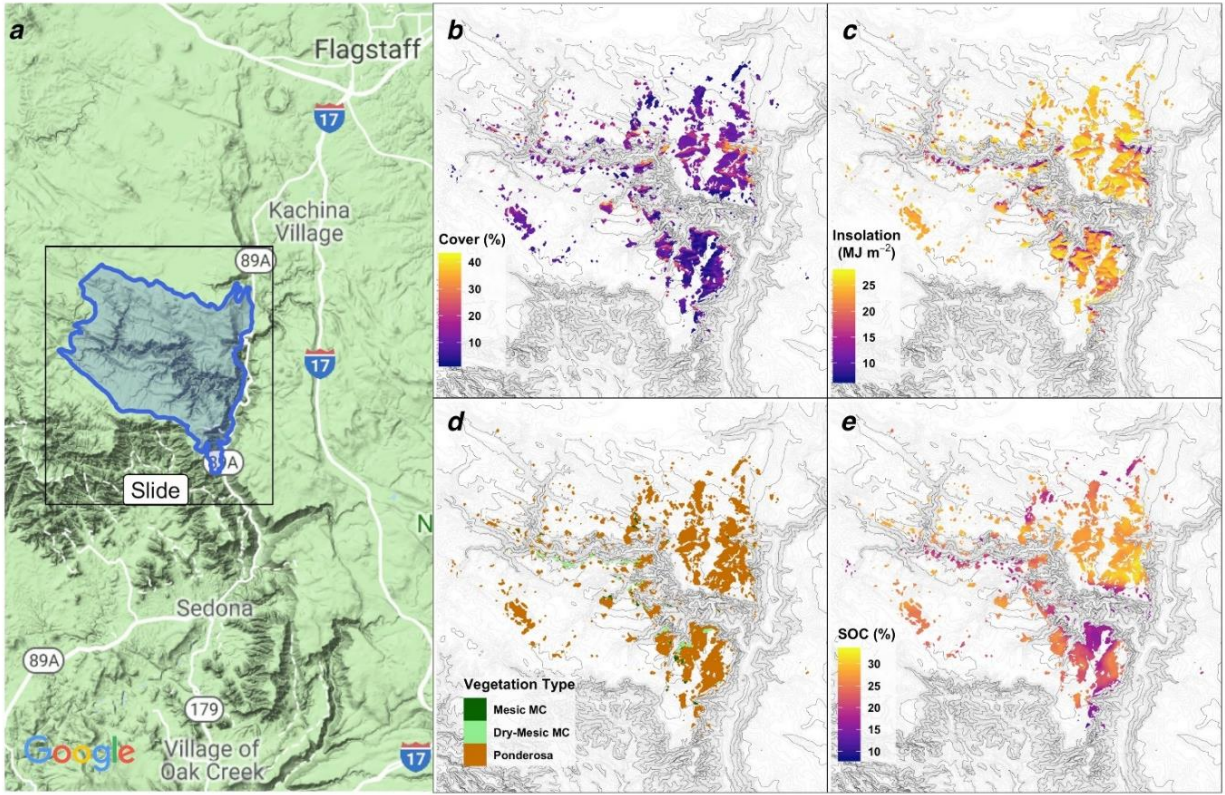


Figure 2.4. A map of (a) the 2014 Slide Fire south of Flagstaff, AZ used for visualizing interactions between the landscape scale predictor variables and their effect on fire moss cover. This map outlines (b) fire moss cover at 2 years after the fire, (c) equinox insolation, (d) pre-fire vegetation type (MC = mixed-conifer), and (e) pre-fire soil organic carbon (SOC).

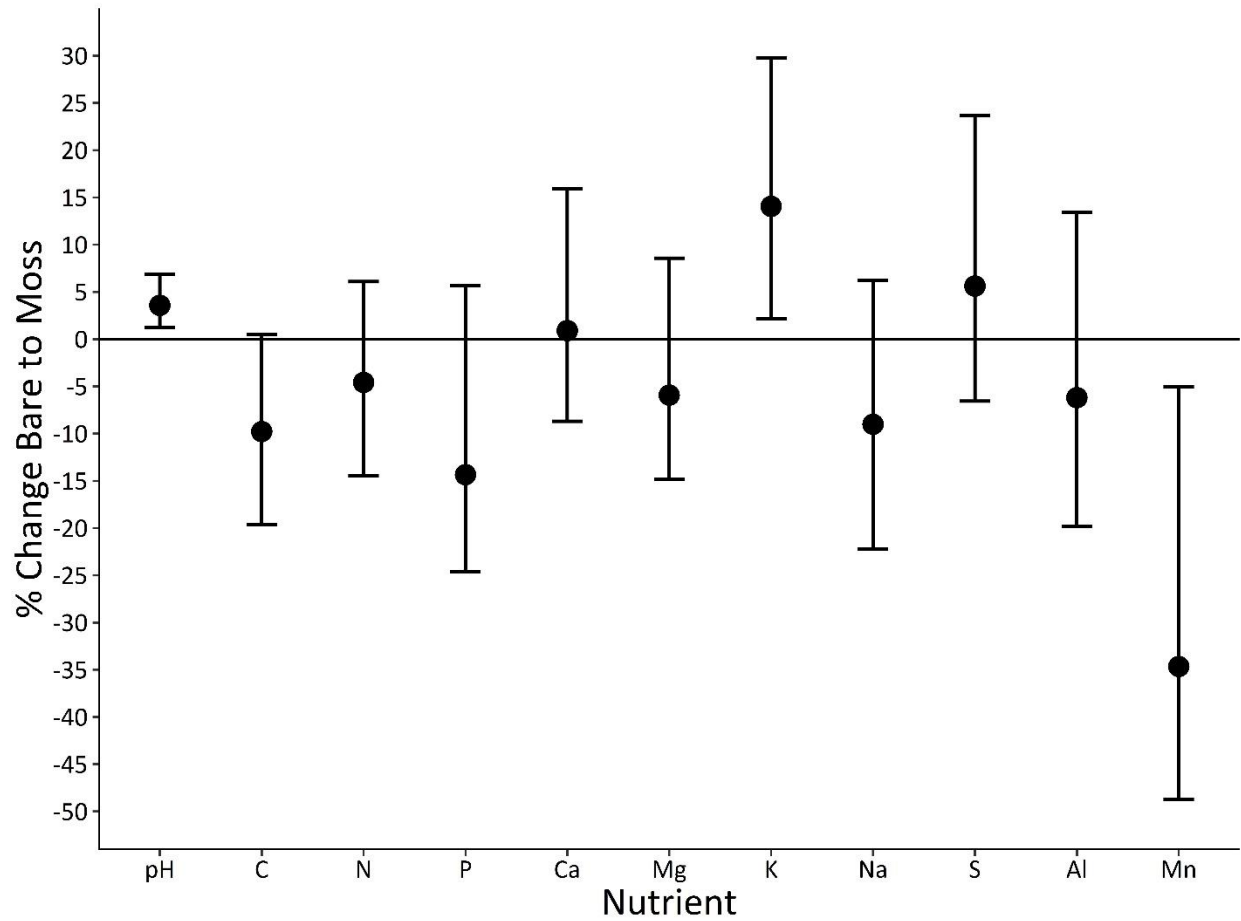


Figure 2.5. Average percent change in pH and nutrient concentration from bare to moss-covered microsites. Error bars are bootstrapped 95% confidence intervals (n = 31).

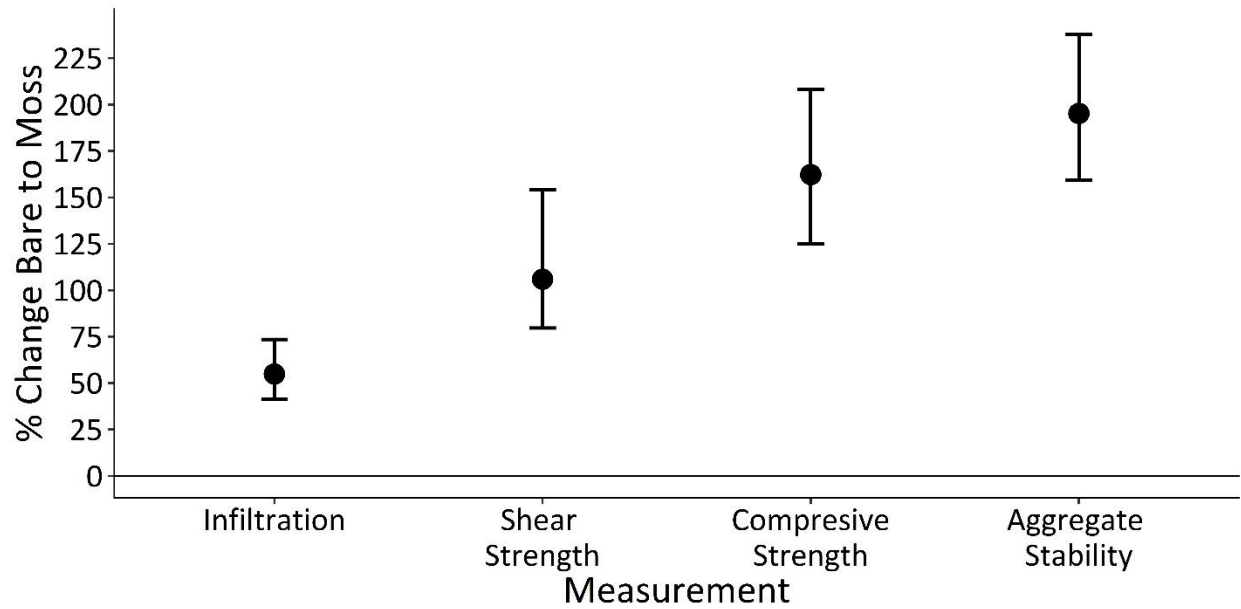


Figure 2.6. Average percent change in hydrological function (infiltration) and erosion resistance (shear strength, compressive strength, aggregate stability) from bare to moss-covered microsites. Error bars are bootstrapped 95% confidence intervals. Infiltration (n=48), shear strength, compressive strength, and aggregate stability (n=50).

CHAPTER III

Improved, scalable techniques to cultivate fire mosses for rehabilitation

Abstract

As wildfires increase in extent and severity in the western United States, land managers need new tools to stabilize and rehabilitate impacted hillslopes. One potential tool is the use of three disturbance-adapted mosses *Ceratodon purpureus* (Redshank), *Funaria hygrometrica* (Cord moss), and *Bryum argenteum* (Silvergreen moss), collectively known as fire mosses. By growing and adding vegetative propagules in the form of gametophyte fragments to burned hillslopes, land managers could potentially increase the rate of moss colonization and stabilize soils. A first step in developing a native plant materials rehabilitation technique is overcoming propagule limitations using *ex situ* cultivation. We focused on greenhouse cultivation of moss gametophyte fragments allowing us to grow vegetative propagules with control over atmospheric, edaphic, and hydrologic conditions. In this experiment, we grew fire mosses using an easily scalable technique and commercially available materials. We demonstrated repeated success growing these species in the greenhouse and fine-tuned harvesting techniques to increase productivity. We found that fire moss achieved high cover in 2 months when grown on organic substrate with constant wicking hydration and a protective shade covering, but growth was not favored by addition of burned materials. We successfully upscaled our growing technique, and developed efficient harvest methods. This success overcomes an initial barrier to testing and developing fire mosses as a novel rehabilitation technique.

Implications for Practice:

- Cultivation techniques outlined in this article can be used to grow three species of moss, collectively known as fire mosses, *ex situ*. These species can be grown rapidly with times to harvest of two months or less.
- Fire mosses are globally distributed early successional species that could potentially be used to rehabilitate both burned and unburned disturbed landscapes.
- By focusing on commercially available materials and scalable techniques, we strived to make this research relevant to researchers and practitioners in the native plant materials development community.

Introduction:

The extent and severity of wildfires in the western United States has increased due to climate change and fire exclusion (Abatzoglou & Williams 2016; Keane et al. 2008; Singleton et al. 2018). This, coupled with development in the wildland urban interface, has increased demand for additional postfire management techniques that can preserve values at risk of postfire flooding such as houses or roads (Robichaud et al. 2014). To mitigate the most immediate of these risks, soil erosion and flooding, land managers use treatments applied to hillslopes. Mulching has proven to be an effective erosion reduction technique; however, it is relatively expensive (Robichaud et al. 2013). Seeding, although comparatively cheap, rarely reduces hillslope erosion due to needed rainfall and time for establishment (Peppin et al. 2010). Exploring rehabilitation using native plant materials beyond vascular plant seeds could plausibly improve success by quickly stabilizing soils while meeting more long-term rehabilitation goals (Robichaud & Ashmun 2013). Alternatives to vascular plant seeding are the disturbance-adapted mosses, *Ceratodon purpureus* (Hedw.) Brid. commonly named “Redshank”, *Funaria hygrometrica*

Hedw. commonly named “Cord moss”, and *Bryum argenteum* Hedw. commonly named “Silvergreen moss” (**Fig. 3.1**), collectively referred to here as fire mosses. These species are widespread and potentially important natural postfire colonizers that share a propensity for rapid proliferation after fire (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982; Hilty et al. 2004; Hoffman 1966). Recent literature suggests that, at high cover, mosses can mitigate erosion in disturbed ecosystems; however more research is needed to test the effectiveness of field inoculation on burned areas (Seitz et al. 2017; Silva et al. 2019; Xiao et al. 2015).

This manuscript details our attempts to grow fire moss vegetatively *ex situ* to overcome propagule limitations (Bowker 2007). Successful cultivation of fire mosses in the greenhouse would be an incremental step toward developing these mosses as a rehabilitation treatment and allow researchers and practitioners to conduct field trials. There have been two previous attempts to cultivate fire moss for rehabilitation purposes with varying degrees of success (Gross 2009; Ives 2016). Gross (2009) initially saw rapid growth of *C. purpureus* and *B. argenteum* on organic rich “topsoil”. However, greenhouse conditions became unfavorable resulting in high rates of moss mortality, likely due to multiple rapid dehydration events (Gross 2009; Proctor et al. 2007). A novel approach to watering allowed Ives (2016) to keep fire moss constantly hydrated, but they did not attain high cover on the mineral substrate used by Doherty et al. (2015) to grow dryland mosses. Building on these studies, we experimentally manipulated three factors: moss community, soil substrate, and amendments of burned material. Previous work suggests that, when grown together, different moss species may either compete for niche space or facilitate each other’s growth (Bowker et al. 2017). We hypothesized that growing two species together

could improve overall cover and tested that hypothesis using the most reproductively distinct early successional mosses. *B. argenteum* has clonal vegetative structures, whereas *F. hygrometrica* reproduces through a protonemal mat (During 1979). Mineral sand did not produce favorable growth (Ives 2016), although organic rich topsoil was a relatively effective substrate (Gross 2009; Ives 2016). We hypothesized that increased organic material could be key to successful cultivation. Finally, we hypothesized that mimicking the postfire environment by adding soil amendments of ash and charcoal could increase moss growth.

After first finding a method that produced rapid moss growth (see **Results: Substrate experiment**), we conducted a second “bulking” experiment, testing two additional factors using a double split plot design. We conducted this bulking experiment while growing all three fire moss species at an increased scale. First, we ground the substrate into a powder, hypothesizing that that could decrease the overall amount of substrate needed for cultivation when compared with unground substrate (an important economic consideration). Second, we added weed cloth below the substrate, hypothesizing that this would simplify drying and harvesting mosses. Our goal was to optimize greenhouse growth techniques and simultaneously produce enough moss to eventually field test these species’ utility as a postfire rehabilitation tool.

Methods:

Field Collection and Processing

F. hygrometrica for the substrate experiment was collected from the Camillo Fire, southeast of Flagstaff, Arizona, November 2015 (34.863940° N, -111.419616° W, 2318m, **Fig. 3.1**). *B. argenteum* was collected in abandoned raised beds outside a USDA Forest Service facility in

Flagstaff, Arizona (35.178237° N, -111.6455066° W, 2098m). In the bulking experiment, all three moss species were collected from burned areas. *F. hygrometrica* was collected from the same location as the substrate experiment and *B. argenteum* and *C. purpureus* were collected from the 2014 Slide Fire (35.025599° N, -111.792511° W, 2118m, **Fig. 3.1**). In both experiments, mosses were dried slowly with a light shade covering to prevent damage due to rapid desiccation (Proctor et al. 2007). Excess soil was removed, and mosses were passed through a 2 mm sieve. Dried mosses were stored in paper bags in the dark for a maximum of 3 months at room temperature (23°C) until experiments began.

Cultivation System

During the substrate experiment, we modified a cultivation system where water is wicked from below (Shaw 1986; Doherty et al. 2015). Water was charcoal filtered then dispersed for 1 min every 4 hours and pooled in the outer basin of a nested basin system, allowing it to stay completely full (Open Sprinkler, Amherst MA, USA). To create the inner basin, 12 x 12 cm, Gladware® containers were filled with 3 cm of Rockwool hydroponic wicking substrate (Grodan Inc., Kingsville, ON, Canada). We then placed 1.5 cm of substrate directly on top of Rockwool and four, 0.5 cm holes were drilled in the bottom of the inner basin to allow water to enter from the outer basin. Holes were drilled halfway up the sidewall of the outer basin to prevent flooding of substrates.

In the bulking experiment, we used six 120 x 55 x 4 cm greenhouse trays and added a row cover (Wellco Industries Inc., Corona, CA) over the entirety of each bulking tray to increase humidity, shade all the trays, and control the spread of fungal gnats. We abandoned the nested basin

design, instead placing Rockwool directly in the tray, reducing infrastructure demands by half without changing water delivery (**Fig. 3.2**).

Substrate Experiment

Using a full factorial experimental design, we manipulated (1) moss species, (2) substrate, and (3) soil amendments. Moss species included three levels: *F. hygrometrica*, *B. argenteum*, and a combination of both species. All were inoculated dry at a rate of 85.4 ml/m². Volume proved to be much easier to standardize across treatments than weight due to the inconsistent density of inoculum. After inoculation, all units were sprayed with water to create a hydraulic connection between moss fragments and substrates. Substrate included two levels: sand mixed with coconut coir in a 50:50 concentration (<https://www.hydrofarm.com/p/JSCCM25>, accessed 1 August 2018) and organic “topsoil” (<http://www.naturescare.com/smg/goprod/natures-care-organic-garden-soil/prod11340017>, accessed 1 August 2018). Substrates were not sterilized prior to inoculation to increase scalability of the results, because sterilization adds labor and could become cost prohibitive at large scales. Soil amendments included four levels: no amendment, commercial wood charcoal (<https://www.wakefieldbiochar.com/shop/wakefield-biochar-soil-conditioner-1-lb-bag/>, accessed 1 August 2018), fully combusted ash from *Quercus gambelii*, and a combination of both. These were homogenized into substrates at a concentration of 4% of total volume. Each of 24 (3 × 2 × 4) treatments was replicated 6 times, for a total of 144 experimental units. To account for unintended colonization of moss within our experiment, we added six uninoculated controls per substrate/amendment combination. The average moss cover value of these controls was subtracted from corresponding units where moss was added to correct for background colonization.

Before inoculation, we collected and analyzed one composite sample of each treatment for total carbon, total nitrogen, phosphate, and pH. Carbon and nitrogen samples were ground using a SampleTek Model 200 Scintillation Vial Rotator with steel tumblers and analyzed using a 4010 Elemental Combustion System (Costech Analytical Technologies Inc., Valencia, CA). Phosphate samples were extracted using the Olsen and Bray methods and analyzed using a Lachat Instruments QuikChem 8500 series Flow Injection Analyzer (Lachat Instruments, Loveland, Colorado, USA). pH was determined using a glass electrode immersed in a saturated paste of 10 mg soil mixed with a .01 M CaCl₂ solution and allowed to stand for 30 min.

Every three weeks and four times over the course of the study, we visually estimated cover to the nearest .5% on each experimental unit. Cover was estimated for the following: living moss to species, senescent moss, bare substrate, and any non-target growth. To increase consistency, one person made all estimates using a reference sheet of cover values. During each sampling period, the outer watering basin of all units was drained, sprayed with alcohol, then scrubbed to reduce contamination. After cleaning, we randomly placed experimental units back into watering basins to limit microclimate effects within the greenhouse. The experiment ran for 63 days from late January to March 2016.

Bulking Experiment

Using six trays as blocks, we tested the addition of weed cloth beneath the substrate and grinding of the substrate. Polyethylene weed cloth (Vigoro Inc., Northbrook, IL) was added to half of each tray above the Rockwool and below the substrate to speed harvesting. Perpendicular to the

weed cloth, substrate ground to a powder in a Wiley mill (Swedesboro, NJ) was added to one half and unground substrate was added to the other half of each tray. This created a total of four treatments (2x2) in each of the six trays. Each tray was inoculated with a mixture of all three moss species at a rate of 20% cover.

To measure moss growth on the bulking experiment, cover of moss and non-target growth was estimated. As opposed to the substrate experiment, we used a point intercept method on a rectangular grid with 30 points per treatment area within each of the six trays. Measurements were conducted every 2.5 weeks until one treatment reached high enough cover that growth was limited by space. The experiment ran for 5 weeks and was sampled twice.

Statistical Analysis

Percent cover change or moss growth (%) from the beginning of the substrate experiment to the last timepoint met statistical assumptions of linearity and equal variance, but not normality. We used a parametric linear model to test factors and two-way interactions of moss species, substrate, and amendment for all treatment combinations. Because our data were not normally distributed, we also used *lmPerm* (Wheeler & Torchiano 2016), to perform a nonparametric permutational ANOVA on the linear model to verify these results. The two sets of results agreed well, so we present the results of the parametric ANOVA, the more widely used method.

In the bulking experiment, we only used cover data from the final sampling timepoint. This met statistical assumptions of normality, equal variance, and linearity. One replicate of the ground treatment with no weed cloth partially flooded due to a thinner substrate and higher capillary

action of the ground organic matter, the rest of the tray was not affected. The replicate experiencing flooding was excluded from the analysis leaving a total of 23 replicates which we analyzed. We analyzed cover data using a mixed effects ANOVA test on a linear model with the main effects of both treatments and the blocking factor (tray). Analyses were conducted using the lmer function in the lmerTest package in R (Kuznetsova, Per Bruun Brockhoff, et al. 2017). For both factors, we explored *post hoc* pairwise comparisons using the lsmeans function in the lsmeans package (Lenth 2016).

Results: Substrate Experiment

Greenhouse Conditions

The greenhouse temperature over the course of the experiment measured 20 cm above the bench ranged from 10-34.5° C with an average of 16.9° C. Relative humidity ranged from 8-74.2% with a mean of 40.9%. Measurements of photosynthetically active radiation and soil surface temperature were taken at midday during a warm period near the end of the experiment, with values of 490 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ and 21.7° C respectively.

Best and Worst Performing Treatments

We found that *F. hygrometrica* grew best on the organic substrate with no amendment added. On this treatment, we saw a 268% increase in cover of *F. hygrometrica* and a final cover of 73.7% (**Fig. 3.3**). *B. argenteum* grew best on organic material amended with charcoal with a 263% increase in cover and a final cover of 73% (**Fig. 3.3**). Adding both species slightly inhibited growth, with the best performing combination being organic material and charcoal and achieving 65% total cover ($F_{[2,126]} = 3.78, p = .025$). The worst performing treatment, with only 6.3% moss

cover, was both species grown together on the sand/coir substrate amended with both ash and charcoal. All moss-treated units started with an initial cover of 20%. By the end of the experiment, background colonization of *F. hygrometrica* had occurred on experimental units that received no moss, with a maximum cover of 3.2%.

Substrate and Amendment Factors

Substrate was a major driver of fire moss growth, with both species preferring organic material over the sand and coconut coir mix ($F_{[1,126]} = 136.5, p < .001$, **Fig. 3.3**). Ash additions inhibited moss growth, with twice as much growth on unamended topsoil and charcoal units as on ash amended units ($F_{[3,126]} = 50.5, p < .001$, **Fig. 3.3**). *F. hygrometrica* grown on organic units amended with ash started to recover by the end of the experiment, but their growth was well behind unamended units (**Fig. 3.4**). On organic soil, the charcoal amendment had a positive effect on *B. argenteum* growth only (**Fig. 3.3**).

Substrate and Amendment Nutrient Concentrations

The organic substrate contained greater than an order of magnitude more total carbon and nitrogen, and twice as much available phosphate as the sand/coir mixture (**Table 2.1**). Amending the soil with ash increased both the phosphate concentration and the pH with the notable exception of the organic ash/char treatment. Charcoal additions resulted in a minor increase in pH but had little effect on nutrient concentrations (**Table 2.1**).

Results: Bulking Experiment

Mosses grew almost twice as fast in the bulking experiment as the substrate experiment. The best performing treatment was unground substrate with no amendment, with a 275% increase in cover in 35 days and a final cover value of 75% (Table S2). Grinding the organic substrate significantly decreased growth with a final increase of only 202% ($F_{[1,15]} = 11.8$, $p = .004$, **Fig. 3.5**). The weed cloth addition inhibited moss growth as well ($F_{[1,15]} = 6.18$, $p = .03$, **Fig. 3.5**); however due to its ability to decouple the moss growing and drying process it allowed us to produce moss that was ready for use more quickly.

Discussion:

Major Drivers of Fire Moss Growth

Moss cover increased more than four-fold in two months under optimal growing conditions provided by the unamended nutrient-rich organic substrate. Fire mosses are completely inactive when dry (Proctor et al. 2007), so growth can only occur during wet periods and is frequently interrupted under field conditions. Our method overcomes water limitation by making hydration, and thus growth, continuous. Our design does not allow us to know why the organic soil was a superior growing substrate, but since hydration level was a constant across substrates, the higher carbon and nutrient content of the organic soil is a likely reason. It was initially surprising that ash substantially inhibited moss growth. However, upon measuring the pre-inoculation pH of ash amended units, it became clear that they were more alkaline than severely burned soils that had received some precipitation (Ulery et al. 1993).

Our method buffers variation in greenhouse climate substantially. The constant wicking method we used stabilized soil surface temperatures when ambient air temperature increased, making maintaining exact greenhouse climate less of a concern. In response to a need for fungus gnat control in the substrate experiment, and hypothesized benefits of humidity conservation, we used row cover in the bulking experiment. We observed that not only did we reduce the spread of fungal gnats with row cover, but also moss leaf survival, height, and sporophyte production were greater than in the previous experiment, creating the potential for greenhouse production of moss spores (HG personal observation, **Fig. 3.6a**). Although row cover was not formally tested as an experimental factor, our observation suggests that it would be worthwhile to investigate further.

Upscaling Cultivation and Improving Harvesting

We have successfully grown all three fire moss species together in large bulking trays that could be upscaled to an entire greenhouse facility. Using bulking trays, we grew mosses four times with an average time to harvest of 2 months. Using this technique, we estimated that in a 100 m² greenhouse one could grow roughly 332 m² of fire moss in one year. It is fortunate that organic substrate was superior because it is common in horticulture and available commercially.

Furthermore, the organic substrate is relatively less dense than the sand/coir substrate, which could reduce transportation and field inoculation costs which are often very high (Napper 2006).

Although the addition of weed cloth slightly reduced growth, it dramatically improved harvesting efficiency by allowing us to decouple growing and drying the moss. Previously, we had to wait for the Rockwool and substrate to dry slowly so as not to damage the moss before harvesting. We can now lift the weed cloth, substrate, and moss directly from the Rockwool.

These materials can be set aside to dry (**Fig. 3.6b**), while setting up the next bulking run. The grinding of substrate did not improve growth rates and made trays more susceptible to flooding due to a thinner substrate with greater capillary action, and thus is not recommended.

Beyond the Burned Environment

Fire moss species' distributions are not limited to burned areas and mosses can be opportunistic colonizers of many disturbed landscapes in a range of ecosystems (Condon & Pyke 2018; Hardman & McCune 2010). To date, these species have been tested as rehabilitation treatments in road construction projects in the Sierra Nevada Mountains (Gross 2009), shrub steppe ecosystems of the Great Basin (Condon & Pyke 2016), and drylands in China (Xiao et al. 2015). These species are also to heavy metal contamination, potentially making them useful in reclamation of industrial sites (Shaw et al. 1989; Shaw 1988). Researchers from Portugal have successfully cultivated *Bryum pseudotriquetrum* (Hedw.) at small scales on organic substrates to restore margins of dam reservoirs (Cruz de Carvalho et al. 2018). This exemplifies that our findings are not limited to the fire mosses discussed in this manuscript and could potentially be used on other disturbance adapted moss species. Exploring the rehabilitation potential of bryophytes is an active field of research and using *ex situ* grown propagules is simplified with the methods developed here.

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Table 3.1. Soil properties for each substrate and amendment combination for substrate experiment.

Substrate	Amendment	Carbon (%)	Nitrogen (ppm)	Phosphate (ppm)	pH
Organic	None	42.23	9800	200	6.36
Organic	Ash	36.07	8700	500	9.51
Organic	Charcoal	44.37	10100	200	6.52
Organic	Ash Char	40.89	9100	200	7.54
Sand Coir	None	2.39	400	20	6.74
Sand Coir	Ash	3.65	400	100	10.51
Sand Coir	Charcoal	2.45	300	20	8.05
Sand Coir	Ash Char	1.75	200	100	10.83

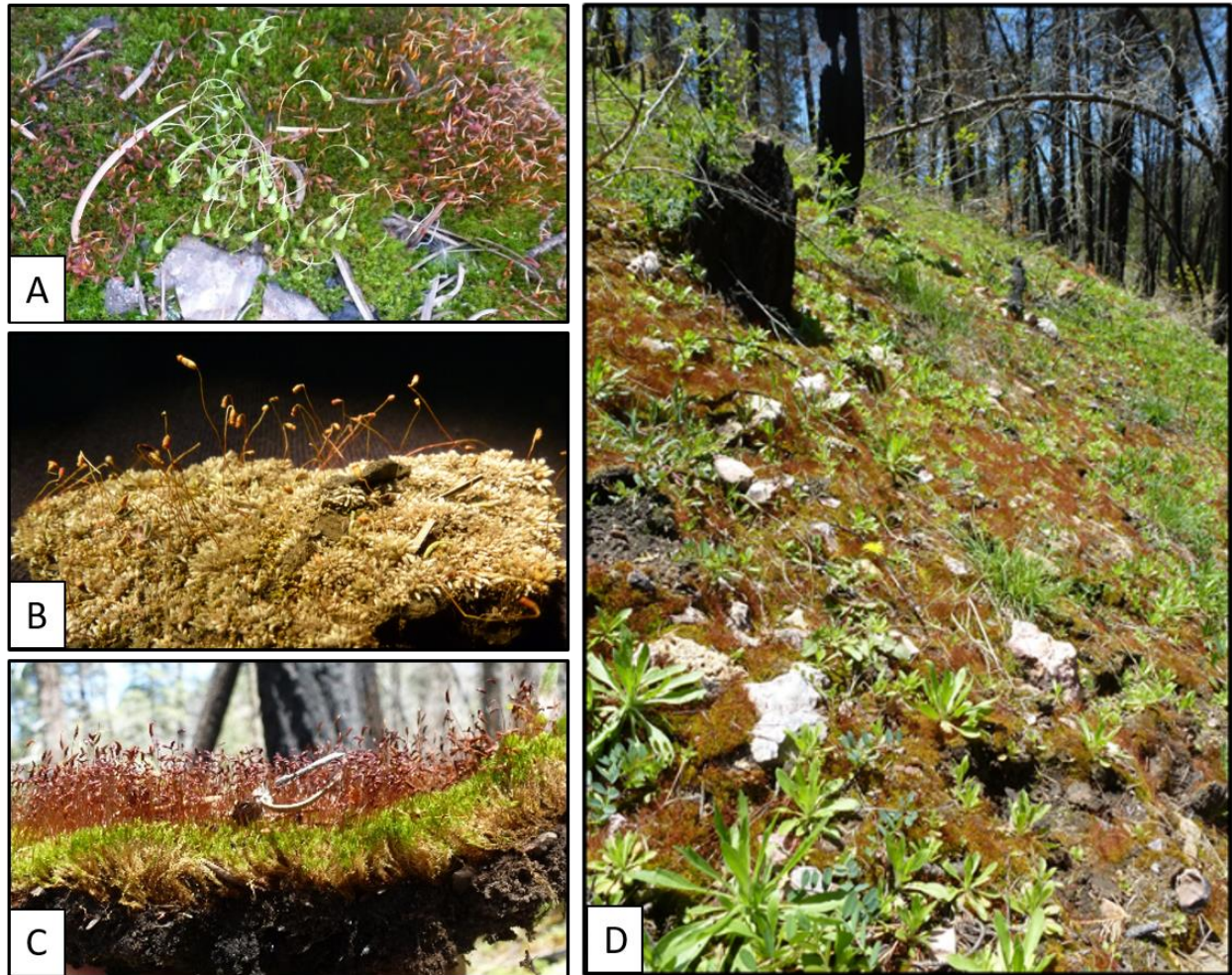


Figure 3.1. The fire mosses, (A) *Funaria hygrometrica*, (B) *Bryum argenteum*, and (C) *Ceratodon purpureus*. (D) Hill slope dominated by *C. purpureus* on 2014 Slide Fire, Oak Creek Canyon, Arizona taken 2 years postfire.

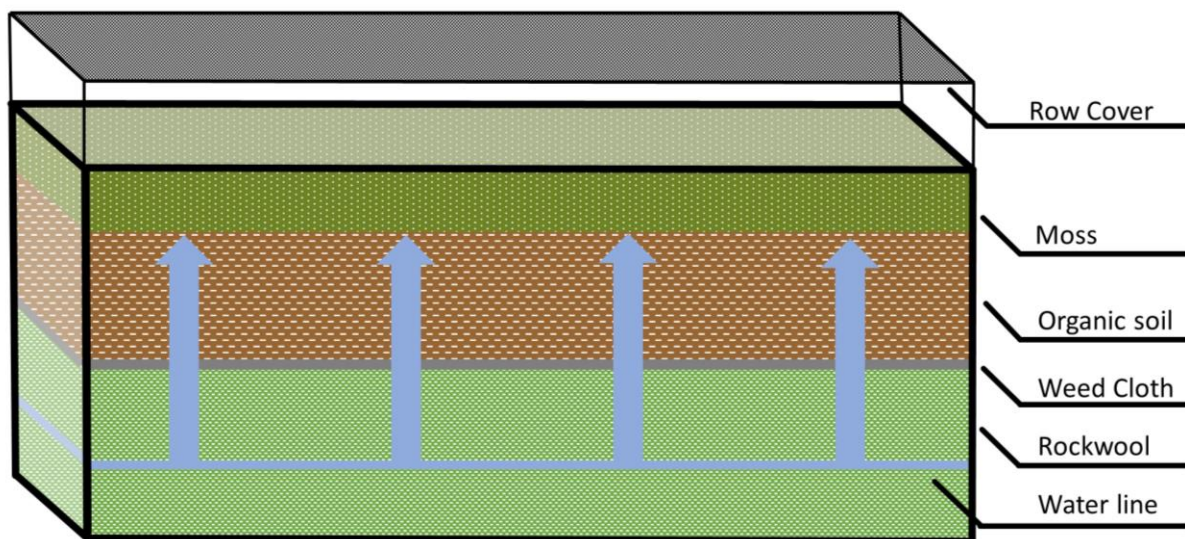


Figure 3.2. Diagram of moss cultivation design used in bulking experiment. Water is ponded in bottoms of basin and wicks from below to keep mosses fully hydrated throughout cultivation. All equipment can be reused in successive cultivation runs.

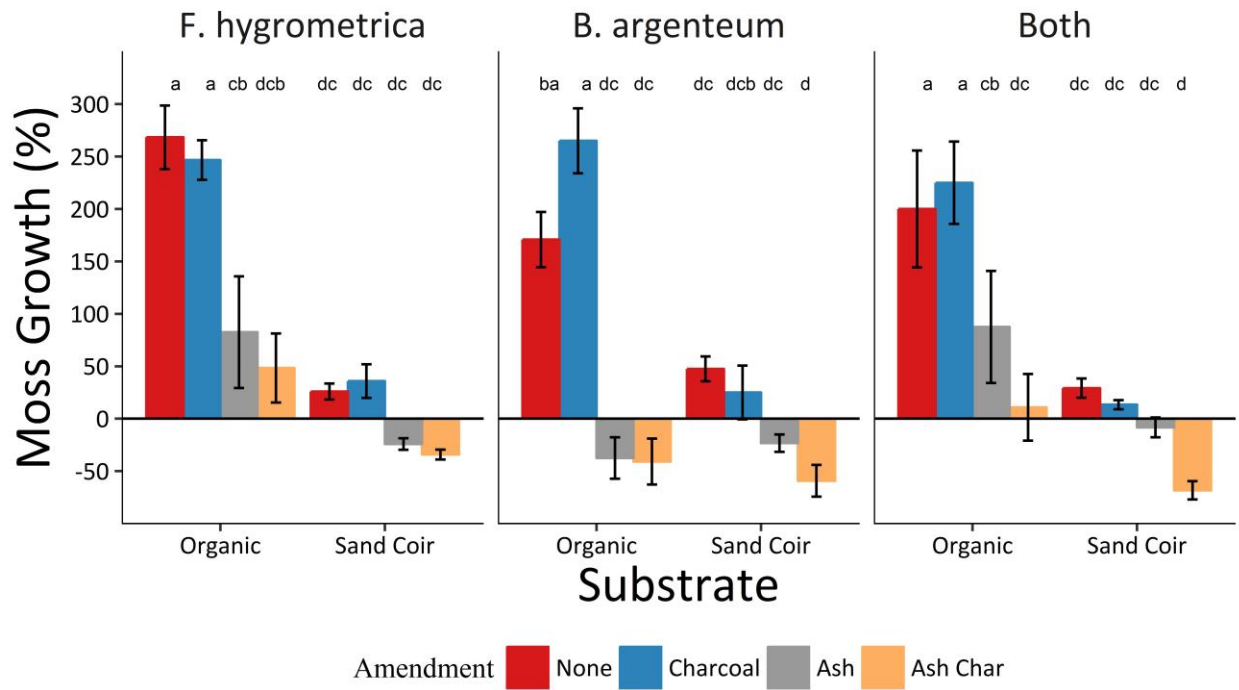


Figure 3.3. Final moss growth in the substrate experiment, expressed as percent increase from original inoculation (negative values signify death). Experimental factors are species, substrate, and amendment. Letter codes represent results of Tukey's corrected pairwise comparisons of treatments (alpha = .05). Error bars represent \pm SE.

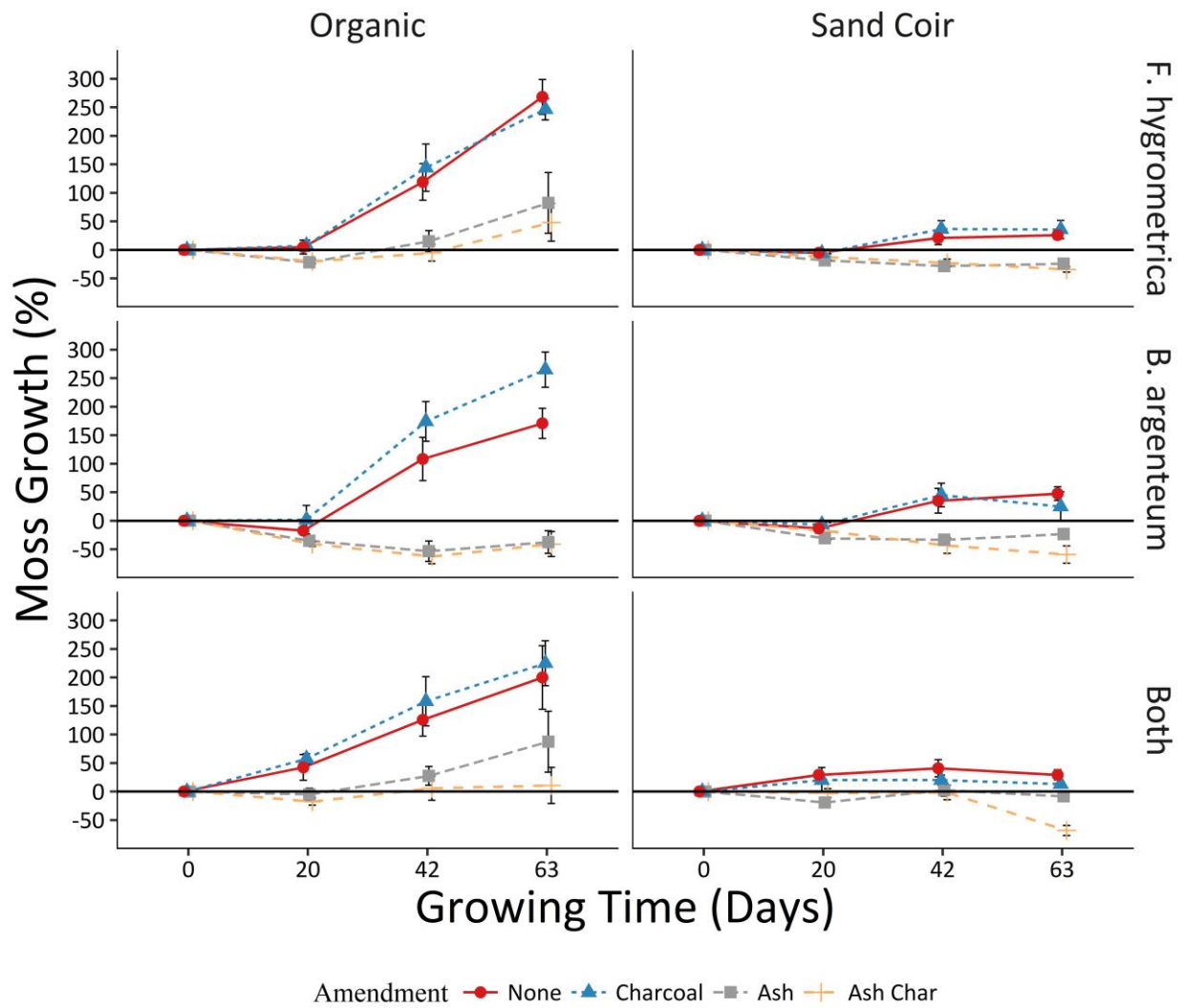


Figure 3.4. Moss growth through time in the substrate experiment, expressed as percent increase from original inoculation (negative values signify death). Experimental factors are species, substrate, and amendment. Error bars represent \pm SE.

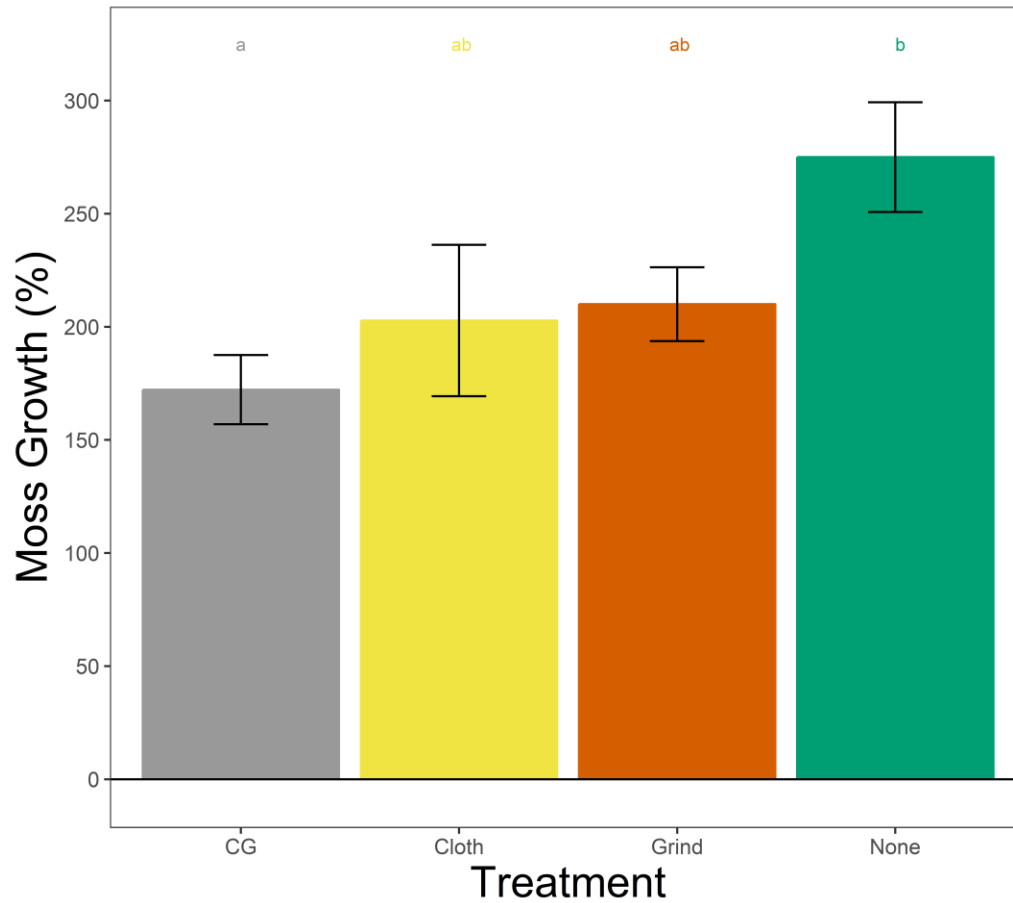


Figure 3.5. Final total moss growth (all species summed) in the bulking experiment, expressed as percent increase from original inoculation (negative values signify death). Experimental factors are weed cloth addition (Cloth) and grinding of substrate (Grind), as well as a combination of both (CG). Letter codes represent results of Tukey's corrected pairwise comparisons of treatments ($\alpha = .05$). Error bars represent \pm SE.

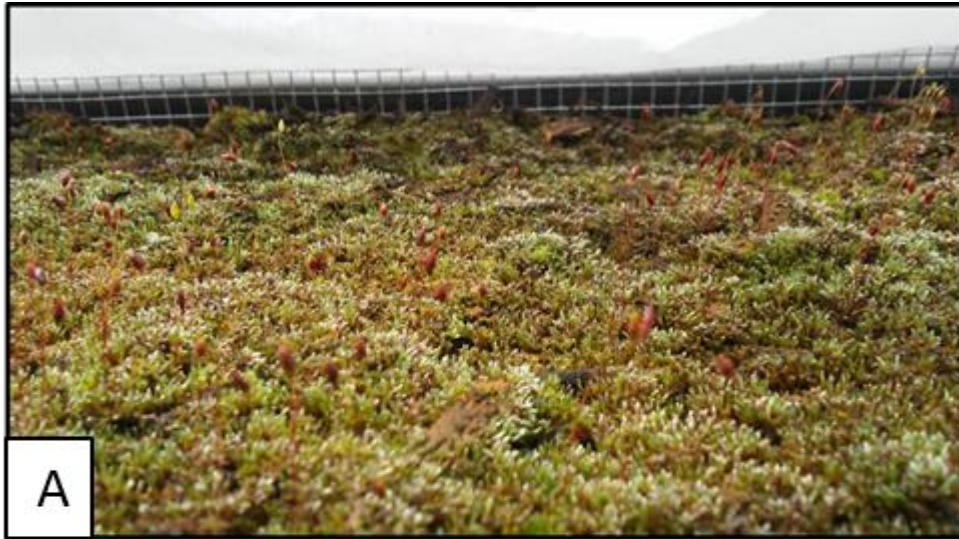


Figure 3.6. (A) *B. argenteum* sporophyte growth in bulking experiment with row cover and (B) greenhouse grown fire moss being dried after removal using weed cloth.

CHAPTER IV

Pelletized inoculation overcomes ant predation and enhances fire moss establishment in severely burned forests

Abstract:

As wildfires increase in extent and severity, new tools are needed to rehabilitate burned landscapes. We tested the effectiveness of adding fire moss tissue, produced in the greenhouse, as a bio-inoculant to severely burned soils. We conducted three sequential experiments using knowledge gained from previous experiments to fine tune fire moss delivery methods. The first two experiments began one week after full containment of a wildfire in a *Pinus ponderosa* forest of Arizona. First, we added disaggregated (passed through a 2mm sieve) moss tissue to burned soil surfaces, which was immediately collected by ants (*Myrmica* sp.). In response to the unexpected herbivory pressure, we added two preparations designed to reduce predation: moss rolled into pellets using diatomaceous earth and moss ground to a powder. Pelletization increased *Bryum argenteum* cover ($F= 35.24$, $p < 0.001$) and the number of distinct moss colonies ($F= 36.83$, $p < 0.001$) when compared to untreated control plots, although cover remained low (1%). The third experiment took place in a mixed conifer forest of New Mexico, USA. Sieved moss, pelletized moss, and pelletized moss at a high (5×) application rate were added to a burned forest, four months after full containment. The high pelletized treatment increased cover to 10% ($F=2.73$, $p=0.046$) after 1.5 years, but treatments largely converged afterward. At both sites, an exceptional drought during the winter of 2017-18 likely dampened moss establishment. Nevertheless, greenhouse-grown moss bio-inoculants, coupled with pelletization, can speed colonization of fire mosses, rendering this approach viable for further refinement and testing.

Implications for practice:

- Insect predation is a novel barrier to moss bio-inoculant survivorship and should be monitored for and potentially mitigated when conducting biocrust restoration trials.
- Pelletization of moss propagules can be effective when attempting to increase cover and should be incorporated into future biocrust restoration research.
- Post-fire moss inoculation may have merit for rehabilitation, but further trials are necessary to improve application techniques and examine bio-inoculant effectiveness in non-drought conditions.
- Rehabilitation using vegetative propagules of *Bryum argenteum* can be successful while both *Funaria hygrometrica* and *Ceratodon purpureus* failed to colonize.

Introduction:

Increases in wildfire extent and severity in the southwestern US due to climate change and elevated fuel densities create a need to rehabilitate severely burned environments (Keane et al. 2008; Singleton et al. 2018; Mueller et al. 2020). Active rehabilitation of vascular plant communities can be an effective management strategy post-fire (Floyd et al. 2006; Ouzts et al. 2015). The effectiveness of using early successional mosses to actively rehabilitate burned areas has not been explored. Three species, *Ceratodon purpureus* (Redshank), *Funaria hygrometrica* (Cord moss), and *Bryum argenteum* (Silvergreen moss), which we refer to collectively as fire mosses, have many traits that could make them a successful and valuable community to promote (Box 1).

Box 1: Moss properties that could allow for colonization post-fire and enhanced ecosystem recovery.

1. As opposed to vascular plants, fire mosses are desiccation tolerant, meaning their vegetative structures can dry out completely without dying and remain viable for years (Werner et al. 1991; Robinson et al. 2000; Li et al. 2014).

2. Fire mosses, especially *B. argenteum*, can reproduce asexually through gametophyte fragments, or specialized tissues (Frey & Kürschner 2011), allowing for a variety of propagule production and delivery techniques.
3. Fire mosses have global distributions, making them a potentially valuable rehabilitation material in burned areas worldwide (Longton 1981; McDaniel & Shaw 2005).
4. Fire mosses can colonize burned landscapes using spores, but cover often remains low (Grover et al. 2020). Active rehabilitation using vegetative propagules could potentially increase that cover (Chen et al. 2009).
5. Early successional mosses can reduce erosion rates in various degraded ecosystems (Xiao et al. 2011; Seitz et al. 2017; Silva et al. 2019).

Our overall objective was to enhance moss cover, and thus recovery, by overcoming propagule limitations through adding greenhouse-grown inoculum (Bowker 2007). Fire mosses can be grown rapidly in a greenhouse using organic substrates, continuous hydration, and climatic controls (Grover et al. 2019), but field establishment has not been tested. Field inoculation success of greenhouse-grown biocrusts in dryland ecosystems of the southwestern US has been limited (Antoninka et al. 2018; Bowker et al. 2019; Young et al. 2019), but we hypothesized that the relatively mesic and colder conditions in burned conifer forests could improve success, as seen in more northerly regions of US (Faist et al. 2019). Field collected moss has also grown well in colder and more mesic environments, especially when combined with organic jute or burlap geotextiles (Condon & Pyke 2016; Slate et al. 2019). However, deployment of propagules to the postfire environment must be rapid and at a large scale to mitigate ecosystem damage (MacDonald & Larsen 2009), because of this we decided to use broadcast techniques which have also been successful (Doherty et al. 2019). To maintain an external source of organic matter that could mimic the positive effects of geotextiles we did not separate moss inoculum from its' cultivation substrate (Grover et al. 2019).

We conducted three sequential experiments using successive knowledge gained from previous experiments to fine tune fire moss delivery methods. In the first experiment (Exp. 1), we crushed dry greenhouse grown moss and organic substrate through a 2-mm sieve and broadcast them on the soil surface, directly after a wildfire in a northern Arizona pine forest. We immediately saw high rates of inoculation predation by ants. In a second experiment (Exp. 2), two treatments were added to prevent predation. We hypothesized that pelletization techniques could reduce predation when coupled with insect deterrents (Madsen et al. 2016; Gornish et al. 2019). We rolled moss into pellets using diatomaceous earth (Quarles 1992) to protect propagules from predation and potentially provide a favorable microsite in which to establish. For the second treatment, we hypothesized that creating very small propagules by grinding inoculum to a powder could reduce predation as they would be less easily targeted by the ants. Alternatively grinding could reduce fitness due to increased erosion of inoculum or decreased survivorship due to smaller, less robust propagules.

A third experiment (Exp. 3) was initiated in a dry mixed conifer forest in New Mexico, USA, using information gained from the first monitoring of Exp. 1 and 2. The pelletized treatment, which had performed well in Exp. 2, was expanded upon. We added pelletized inoculum at a similar rate to Exp. 2 and at 5× the volume. Our ultimate objective of fire moss inoculation is to expedite the recovery of ecosystem function and reduce soil erosion (Grover et al. 2020). We hypothesized that 5× inoculation would induce high rates of moss colonization, allowing us to test mosses contribution to hydrological function and erosion resistance at the plot scale (Seitz et al. 2017; Silva et al. 2019). We did not add ground moss as it had experienced relatively low initial establishment success on Exp. 2. These initial tests of field inoculation of greenhouse

grown fire mosses provide valuable information in developing this and other biocrust inoculation techniques.

Methods:

Study Site Descriptions:

We conducted Experiments 1 and 2 on the Boundary Fire, which began on 01 June 2017, 33.5 km northwest of Flagstaff, Arizona, USA. The Boundary Fire was 7200 ha and burned primarily in heavy downed fuel within the perimeter of a previous burn, the 2000 Pumpkin Fire. We selected study sites that experienced moderate to high soil burn severity, as determined by the Burdened Area Emergency Response assessment team, as they have the highest potential for post-fire erosion and hydrologic disfunction (Parsons et al. 2010; Moody et al. 2013). Exp. 1 contained only dead and down fuel before the Boundary Fire (35.42524588° N, -111.88336642° W, 2469 m). Exp. 2 had been planted with ponderosa pine seedlings after the 2000 Pumpkin Fire and soil burn severity was higher than in Exp. 1 due to elevated fuel densities pre-fire (35.42848517° N, -111.8827725° W, elev 2451 m, **Fig. 4.1a**). Soils in Exp. 1 and 2 are Ustolls derived from a Rhyolitic parent material with a silt loam surface texture (0-1cm) (Kettler et al. 2001; Ramcharan et al. 2018). Average precipitation and temperature are 671 mm and 7 °C respectively, with cold wet periods occurring from Nov-Mar and warm wet periods occurring from July-Aug (Daly et al. 2008).

We installed Exp. 3 on the Cajete Fire in the Jemez Mountains of northern New Mexico. The fire began 15 June 2017 and burned 570 ha, 13.5 km northeast of near Jemez Springs, NM. It was contained on 24 June 2017. Our study site was in a 2.3 ha patch of high soil burn severity at the

northern edge of the fire (35.818068° N, -106.554721° W, elev 2607 m, **Fig. 4.1c**). Soils are Ustoll suborder derived from a Rhyolitic parent material with a loam surface texture (0-1cm) (Kettler et al. 2001; Ramcharan et al. 2018). Average precipitation and temperature are 625 mm and 5.9 °C respectively, with constant precipitation from Sep-June and warm wet periods occurring from July-Aug (Daly et al. 2008).

Plot Installation:

We targeted patches of high soil burn severity during plot installation for all experiments to reduce heterogeneity of experimental units (Parsons et al. 2010). We selected low slope angles (<10 %) to reduce loss of bio-inoculants to erosion. Plots consisted of a 1 x 1 m quadrat with permanent iron stakes placed at the northeast and southwest corners. Exp. 1 began on 5 July 2017 and Exp. 2 on 12 July 2017. One major rain event occurred between site installations, but both sites were installed at the beginning of the summer monsoon season. Exp. 3 was installed on 4 Nov 2017 four months post fire.

Moss collection and cultivation:

For Exp. 1 and 2, we sourced *F. hygrometrica* from the 2016 Camillo Fire, southeast of Flagstaff, Arizona, November 2016 (34.863940° N, -111.419616° W, 2318 m). We sourced *B. argenteum* and *C. purpureus* from the 2014 Slide Fire (35.025599° N, -111.792511° W, 2118m). For Exp. 3, we collected only *B. argenteum* and *C. purpureus* from the 2013 Thompson Ridge Fire (35.893059° N, -106.577049° W, 2711 m). In all experiments, mosses were dried over a period of 10 or more days, with a light shade covering to prevent damage due to rapid desiccation (Proctor et al. 2007). Excess soil was removed, and mosses were crushed through a

2mm sieve to break up colonies. Dried mosses were stored in paper bags in the dark at room temperature (23 °C) until used to produce more biomass in the greenhouse as a bio-inoculant.

Cultivation:

We cultivated mosses in the greenhouse using the methods outlined in the bulking experiment of Grover et al. (2019). Briefly, they were dispersed on an organic soil and kept moist continuously in a climate-controlled environment. When moss cover exceeded 80 %, moss and organic substrate were dried slowly under shade cloth in the greenhouse, then crushed through a 2-mm sieve. Moss was not separated from the substrate to maintain an external source of favorable nutrients during inoculation. Inoculum was placed into a bucket and stored at room temperature (23 °C) for no more than 3 months until field experiments commenced.

Experimental design:

In Exp. 1 we replicated treatment levels of untreated control and sieved moss 15 times and randomly assigned to plots ($n = 30$). During application, we scooped moss out of a bucket using a 250 ml cup and shook it evenly onto each plot. Prior to and periodically throughout the inoculation process, we stirred moss to prevent settling.

In Exp. 2 we replicated four treatment levels of control, sieved moss, moss pellets, and ground moss 12 times and randomly assigned them to plots ($n = 48$). For each replicate of each treatment, we applied 250 ml of sieved moss inoculum from the bucket in the same manner as Exp. 1. The sieve treatment matched Exp. 1 exactly. Moss pellet replicates were made individually. We mixed moss with diatomaceous earth (1:1 by volume) in a 20-liter bucket. Using a hand pump sprayer, we periodically added a fine jet of water to the mixture while rotating the bucket from

the handle. This had the effect of rolling the mixture into unequal sized pellets ranging from > 1 to 15 mm in diameter which were then dried slowly in the greenhouse (**Fig. 4.2b**). We stored replicates in individual paper bags until shaking them evenly onto plots during inoculation. For the final treatment we ground moss to a fine powder using a mill (Thomas[®] Wiley Mill, Swedesburo, New Jersey, USA), and stored them separately and shook evenly onto plots.

In Exp 3 we applied four treatment levels of control, sieved moss, pellets at a similar volume to Exp. 2, and moss pellets at five times the volume of Exp. 2 (hereafter pellet 5×), replicated 12 times and randomly assigned to each plot (n = 48).

Monitoring:

We monitored every spring and fall when mosses were dry. We divided plots into 4 quadrants and HG visually estimated cover to the nearest 0.1% on each quadrant for all visits (Kercher et al. 2003). Visual estimation is particularly accurate when the class of interest is at relatively low cover, as was often the case with our mosses (Meese & Tomich 1992). A reference sheet illustrating cover amounts was used for consistency. Basal cover classes were: moss to species, moss protonema, bare soil, rock, litter, and vascular plant. Canopy cover classes were: forb, graminoid, shrub, and tree. This monitoring occurred once for Exp. 1 and concluded in fall 2017, five times for Exp. 2 and concluded in fall 2019, and three times for Exp. 3 and concluded in spring 2019.

Initially, while cover was low, we counted the number of distinct moss colonies in each plot quadrant as a measure of colonization events (Doherty et al. 2019). A colony was defined as a

spatially discrete patch of moss that we interpreted as having radiated from a central colonization event of a single propagule. Physical separation between patches could be no less than 2 mm. If moss colonies were found in a quadrant where the visual estimates had recorded no moss, we changed the cover value to one half of the lowest cover value (0.05 %). This allowed us to more accurately differentiate low cover from true absences using the more precise colony count method. For both cover and colonies, quadrant level data was aggregated to the plot scale before analysis.

In fall 2019 we attempted to apply the above techniques to monitor both cover and colony counts on Exp. 3. However, high rates of annual vascular plant growth and seed dispersal obscured our plots, preventing accurate estimates (**Fig 4.1d**). In lieu of the previous methods, we estimated moss cover of Exp. 3 with a point intercept method using a 40 x 40 cm gridded frame and reading 50 points per plot, and we did not attempt to count colonies.

Post inoculation quantification of drought:

To understand how post inoculation weather was driving inoculation success, we extracted drought severity values for Exp. 2 and 3. We used Google Earth Engine to extract Palmer Drought Severity Index (PDSI) at a spatial resolution of 4 km and a temporal resolution of 10 days as generated by Abatzoglou et al. (2014). PDSI accounts for both precipitation and potential evapotranspiration and is highly comparable within regions such as our study sites (Dai 2011). PDSI is often reported from < -4 (Exceptional Drought) to > 4 (Exceptionally Moist) but more extreme values are possible.

Soil sample analysis:

At the time of inoculation, we took a composite soil sample with > 10 subsamples throughout the study sites for Exp. 2 and 3 at a depth of 0-1 cm. We sieved samples to 2 mm and analyzed them for pH, total carbon and nitrogen, available phosphate, and a suite of available cations and trace metals, following the Forest Inventory Analysis Protocol (Amacher et al. 2003). We determined pH using a glass electrode immersed in a saturated paste of 10 mg soil mixed with a 0.01 M CaCl_2 solution and allowed to stand for 30 min. To test for total carbon and nitrogen content, we ground and analyzed samples using a 4010 Elemental Combustion System (Costech Analytical Technologies Inc. Valencia, CA). We extracted phosphate using the Olsen ($\text{pH} > 6$) and Bray ($\text{pH} \leq 6$) methods and analyzed using a Lachat Instruments QuikChem 8500 series Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA). We extracted water soluble cations and metals using a 1M NH_4Cl solution. We used an argon gas carrier and analyzed samples on a Thermo ScientificTM iCAPTM 7000 Series ICP-OES (Inductively Coupled Plasma-Optical Emission Spectrometry) or mass spectrometry (ICP-MS), using QtegraTM ISDSTM Software. Cations and metals consisted of calcium, magnesium, potassium, sodium, sulfur, aluminum, and manganese.

Statistical analysis:

All statistical analyses for this manuscript were conducted in R version 3.6.1 (R Core Team 2019). To analyze Exp. 1, we bootstrapped linear models to create 95 % confidence intervals of mean moss cover. We used the boot package (Canty 2002) to perform residual resampling and stratified by treatment levels. This method is robust to non-normality and unequal variance in residuals (Canty 2002), both of which occurred in our dataset.

To analyze Exp. 2 and 3 we conducted two 2-way ANOVAs on linear models with a fixed effect of treatment and a random effect of sampling date. The first linear model had a response of moss cover while the second had a response of moss colony count. To satisfy model assumptions of equal variance and normality we performed a cube root transformation on all response variables before conducting our analysis. Analyses were completed using the lmerTest package creating a type three ANOVA table with a Satterthwaite's degrees of freedom calculation (Kuznetsova et al. 2017). In Exp. 2, one replicate in the grind treatment was a strong outlier with >30 times the average moss cover in spring 2019. We concluded this was due to convergent overland flow depositing moss from other plots onto this plot and excluded it from cover and colony analyses.

Results:

Experiment 1:

When inoculating Exp. 1 we immediately saw ants (*Myrmica* sp.) pick up pieces of moss and remove them from the plot (**Fig. 4.2a**). By the time we had finished setting up the experiment (~1 hr), we returned to the first treated plots and searched for moss propagules. No sign of the inoculum or the ants could be found. In the Fall 2017 monitoring of Exp.1 we found that treated plot cover (mean = 0.11, 95% CI = 0.013-0.33) did not differ from control cover (mean = 0.01, 95% CI = 0.00-0.08) and concluded that moss colonization was precluded by the ant predation. No further monitoring was conducted.

Experiment 2:

In Exp. 2 pelletization was the most successful treatment (**Fig. 4.2b-c**), increasing *B. argenteum* cover ($F=35.24$, $p<0.001$) and colony count ($F=36.83$, $p<0.001$) compared to the control (**Fig. 4.3a-b**). However, the highest pelletized mean cover value was low, $1.0 \pm 0.4\%$. The worst performing treatment was sieved moss with a maximum mean cover of $0.2 \pm .1\%$ where we also saw high rates of ant predation immediately after inoculation. Background colonization of *B. argenteum* on control plots was lower still, reaching a mean of $0.1 \pm .05\%$ cover by the end of the experiment. During the first three monitoring visits we found no colonization of *C. purpureus* on any treatment, but by May 2019 trace amounts were observed on pellet and grind treatments. We found no *F. hygrometrica* on any treated plot.

Experiment 3:

One week after inoculation, the study site had received 26 mm of rain. No trace of the diatomaceous earth was detectable, and pellets had disintegrated onto the soil surface (**Fig. 4.2c**). *B. argenteum* colony counts at the first monitoring visit were high on pelletized plots with a mean of 93 per m^2 (**Fig. 4.3b**). The number of colonies declined with subsequent monitoring between fall 2017 and fall 2018, then leveled between fall 2018 and 2019 with an average colony count of roughly 30 per m^2 . This decline corresponds with an exceptional drought that occurred over the winter of 2017/2018 with PDSI values below -4 (**Fig. 4.3c**).

In Exp. 3 pelletization at 5 \times volume was the most successful treatment in Exp. 3 with *B. argenteum* reaching a maximum mean cover of $10.5 \pm 2.5\%$ in June 2019 ($F=2.73$, $p=.046$, **Fig. 4a**). The sieve and pellet treatments had similar cover values throughout the experiment and

performed only slightly better than the controls (Fig 4.4a). Natural recruitment on control plots of *B. argenteum* was high compared the Exp. 1 and 2, reaching a maximum cover of $6.8 \pm 2.3\%$ in June 2019. Moss cover at the first monitoring visit, six months after inoculation, was undetectable on any plot; however, pellets were still visible. This is most likely due to the exceptional drought that occurred over the winter of 2017/2018 (**Fig. 4.4c**). As treatment cover did not strongly diverge from controls in this experiment, we opted not to test for moss associated soil hydrologic and erosion functional differences at the plot scale. *C. purpureus* was detected on one pelletized and one sieve plot at the final monitoring visit. No *F. hygrometrica* was found at any time.

In contrast to Exp. 2 the number of colonies for all treatments in Exp. 3 increased through time (**Fig. 4.4b**, $F=3.96$, $p=0.01$). In spring 2018 there had been so little precipitation that pellets were intact, and diatomaceous earth was still visible making it difficult to assess colony counts. Strong monsoon precipitation in 2018 lead to a large increase in colony counts by the fall 2018 monitoring (**Fig 4.4b-c**). The colony count number plateaued from fall 2018 to spring 2019 however there was a relatively large increase in cover during that time period (**Fig. 4.4a**).

Soil nutrient levels at inoculation differed between Exp. 2 and 3. Soil carbon and nitrogen were roughly twice as high on Exp. 2; however, Exp. 3 generally had higher cations and trace metals (**Table 4.1**).

Discussion:

Insect predation may be a barrier to moss rehabilitation:

The immediate failure of sieved treatments in Exp. 1 and 2 highlights insect predation as a previously unidentified barrier to biocrust restoration success (Bowker 2007), and merits further study. To our knowledge, no work has quantified the effect of insect predation on biocrust inoculum. However, biocrust inoculum predation has been documented anecdotally in Bandelier National Monument close to our New Mexico study site (K. Young personal communication, Young et al. 2019). Seed predation by ants can be higher in summer which aligns with the inoculation timing of Exp. 1 and 2 (Pol et al. 2011; Suazo et al. 2013). We looked for, but did not see, ant predation on sieve treatment plots in Exp. 3, which was inoculated in early November. Other factors such as a smaller patch of high severity, or a longer time after fire in Exp. 3 could have contributed to lower predation. Fall biocrust inoculation has also been suggested due to more favorable growing conditions in winter (Condon & Pyke 2016; Bu et al. 2018).

Pelletization overcomes barriers to colonization:

Learning from the failure of Exp. 1, we set out to reduce moss predation through pelletization and grinding moss to a fine powder. Pelletization has had mixed results in vascular seed restoration trials, but is often successful at preventing seed predation (Gornish et al. 2019). Diatomaceous earth has been used previously for pelletization of graminoids in a greenhouse experiment but its role was primarily as a binder and was not intended as an insect-deterrent (Madsen et al. 2014). By encasing moss propagules inside diatomaceous earth, we restricted ants' access to them, but diatomaceous earth is only effective when dry (Quarles 1992). In Exp.

2, inoculation occurred at the onset of monsoon season and diatomaceous earth was quickly washed away by rainfall. In Exp. 3 pellets remained visible on the plot for > 6 months, due to the drought, potentially increasing mosses long-term viability in those conditions. To our knowledge, this is the first use of a pelletizing agent to enhance moss colonization and its relative success in establishing moss suggests there may be merit in broader investigation of pelletization technology (Madsen et al. 2016; Gornish et al. 2019). Grinding of moss propagules did initially increase colonization on Exp. 2, but to a lesser extent than pelletization, so we do not recommend its use as a bio-inoculant preparation technique.

Potential benefits of pelletization extend beyond predation deterrence:

One potentially major barrier to successful moss rehabilitation is wind and water erosion due to the relatively low density and small size of inoculum particles (Bowker 2007). This is of concern on severely burned hillslopes where erosion rates can be extremely high (Scott et al. 2009). If propagules are not rapidly attached to the soil surface, they can be transported off plots. By encasing moss within a pellet, we were able to increase the density two-fold and attach it to the soil better (**Fig. 4.3c-d**), potentially reducing the risk of loss due to erosion. Additionally, pelletization could be useful when integrating biocrust rehabilitation with current seeding techniques such as mechanized inoculation (Doherty et al. 2019). Practitioners struggle when attempting to evenly apply seeds of varying densities due to stratification within hoppers, and pelletization was suggested as an effective way of overcoming this issue (Masarei et al. 2019). Doherty et al. (2019) found that mosses tended to jam in the tubing of a drill seeder. We hypothesize that, by pelletizing moss and seed together, issues of stratification and jamming could be remedied, although more research is required to confirm this.

Moss species traits affect establishment success:

B. argenteum was the only species to successfully establish in Exp. 2 and 3. We believe this may be related to specialized asexual reproductive structures formed by *B. argenteum* that are not found in either *F. hygrometrica* or *C. purpureus* (Rosentreter 2019). Rosentreter (2019) suggests using moss spores for rehabilitation of those species, which we did not attempt. In a greenhouse setting, all three species were successfully cultivated from gametophyte fragments when water limitations were removed so drought likely contributed to this failure in the field (Grover et al. 2019). Conversely, we found that *B. argenteum* is resistant to exceptional drought, thus we might hypothesize that specialized asexual propagules allow the species to persist through drought events when vegetative tissue of the other species cannot. Finally, we saw a cyclic pattern in *B. argenteum* cover with growth in winter and subsequent loss in summer. This cyclic pattern agrees with biocrust growth in drylands (Bu et al. 2018) and is further evidence that late fall inoculation could increase success.

Conclusions:

This research demonstrates incremental success in bio-inoculation of greenhouse-grown mosses on recently severely burned forests. These methods successfully established *B. argenteum* on two different wildfires in the southwestern US by pelletizing mosses and organic substrate with diatomaceous earth. Moss cover however remained low, likely due to an exceptional drought which occurred in the first winter after inoculation. Furthermore, we highlight a potentially novel barrier to biocrust restoration success, insect predation, and a propagule delivery method that appears to overcome that barrier, pelletization. Future biocrust restoration research should

attempt to quantify insect predation and account for or mitigate it when necessary and broaden investigation of pelletization techniques and inoculation rates.

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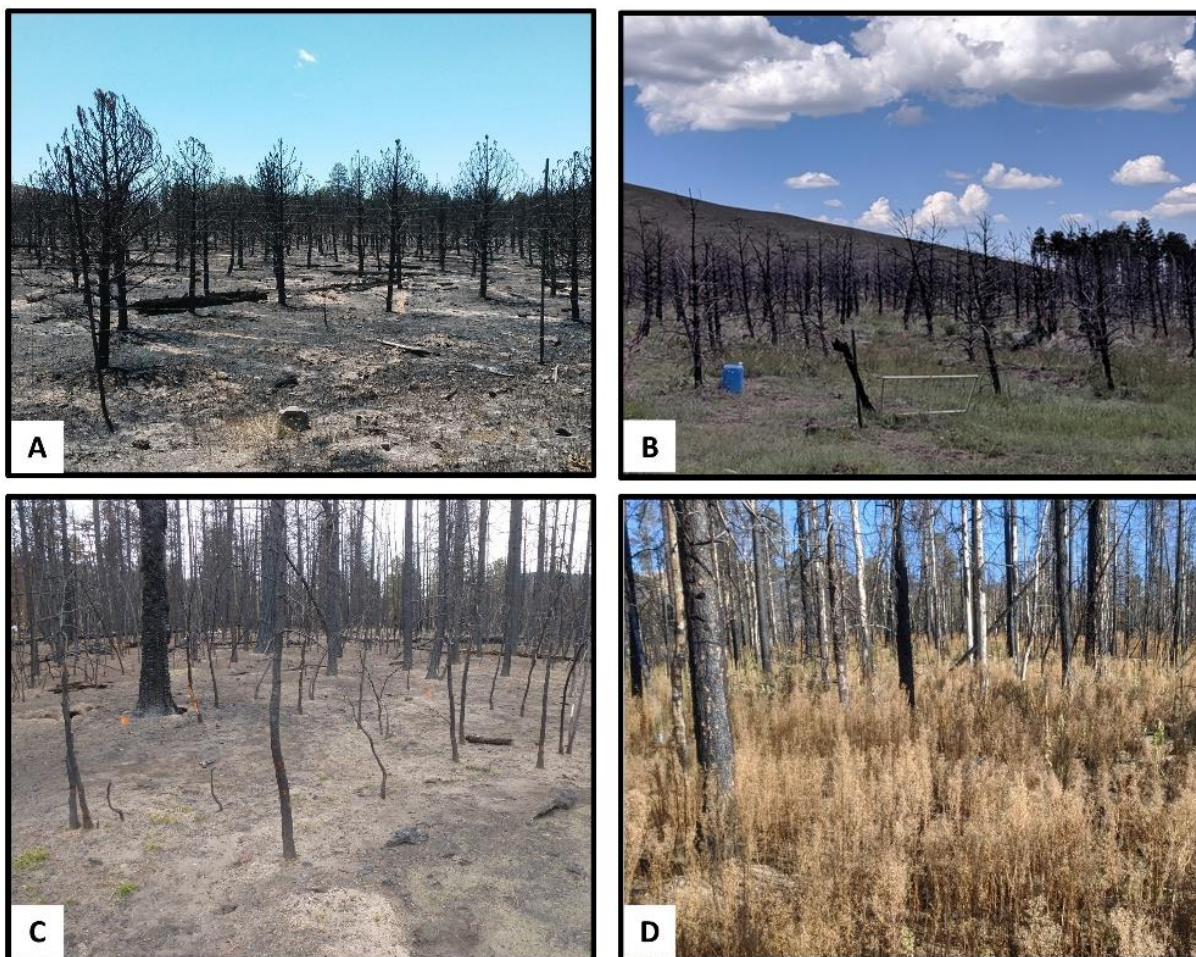


Figure 4.1: (A) Exp. 2 directly after fire, prior to inoculation, (B) two years after inoculation, (C) Exp. 3 four months after fire, prior to inoculation, and (D) two years after inoculation.

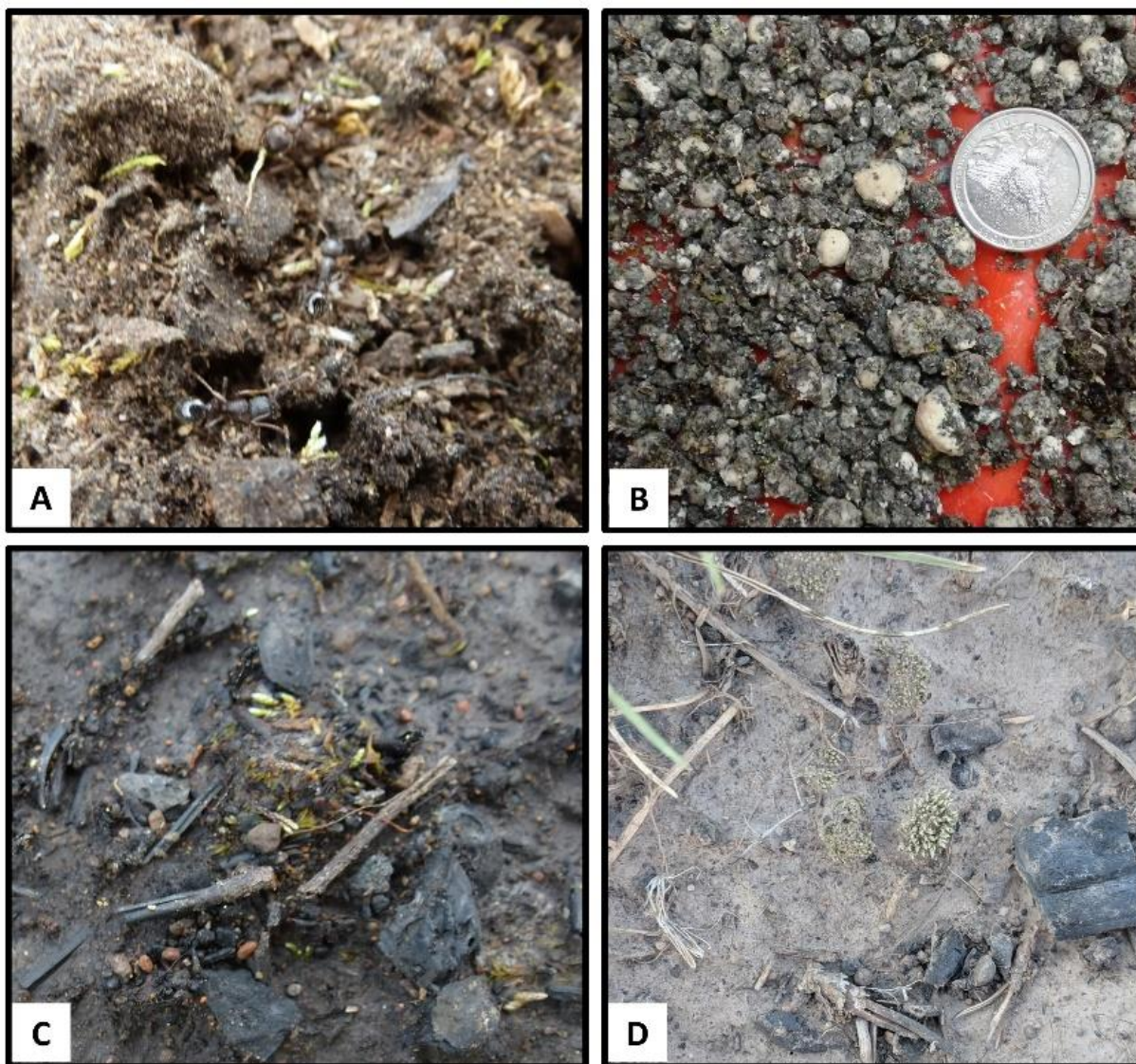


Figure 4.2: (A) ants (*Myrmica* sp.) collecting sieved inoculum on Exp. 1, (B) Pelletized moss prior to inoculation, (C) one week after inoculation and (D) one year after inoculation.

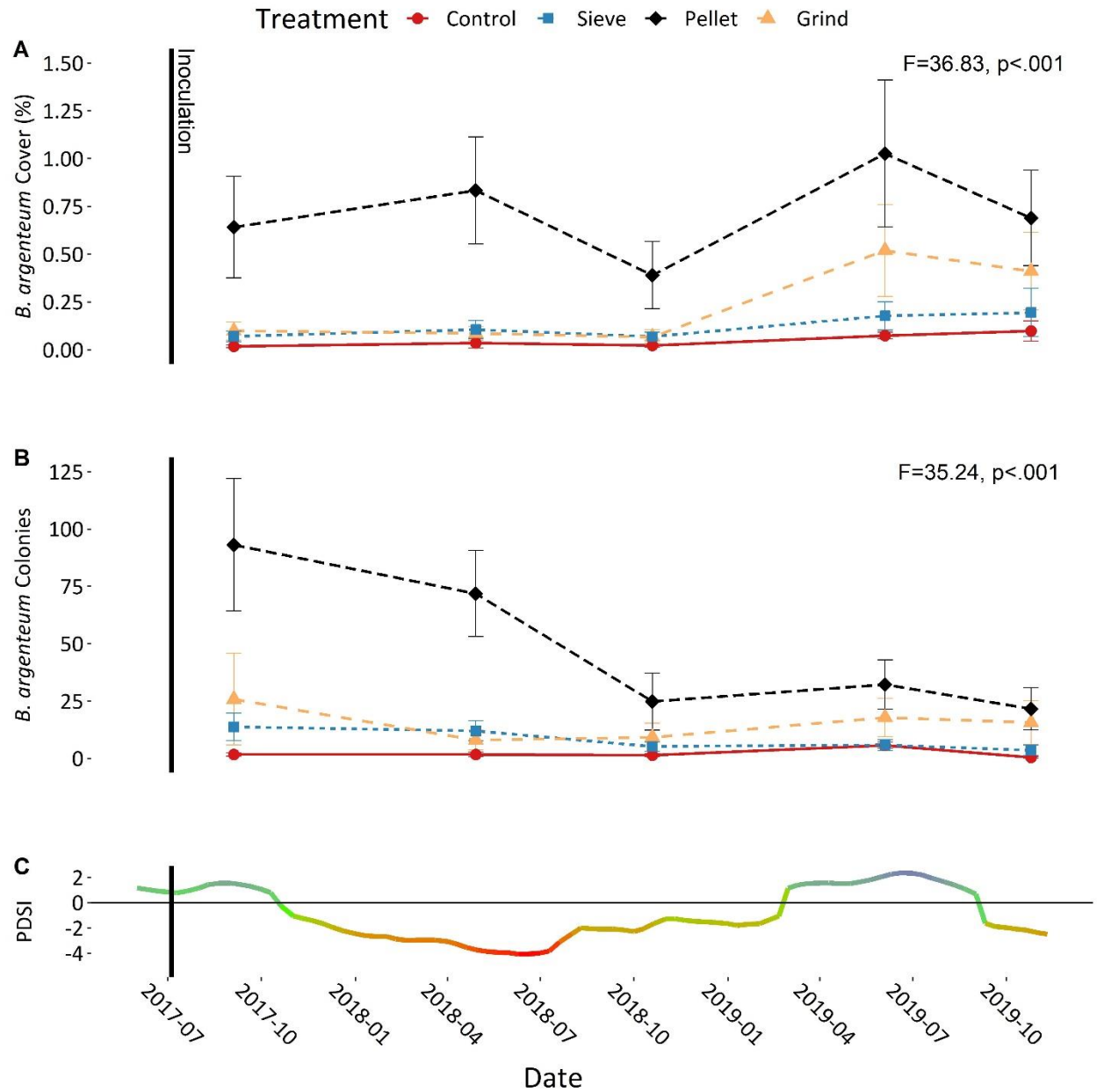


Figure 4.3: Exp 2, vertical lines indicate date of inoculation. (A) *B. argenteum* cover and (B) colony count at monitoring visits. (C) Palmer drought severity index (PDSI) throughout the experiment, negative values indicate drought while positive indicate moisture. Error bars represent \pm SE

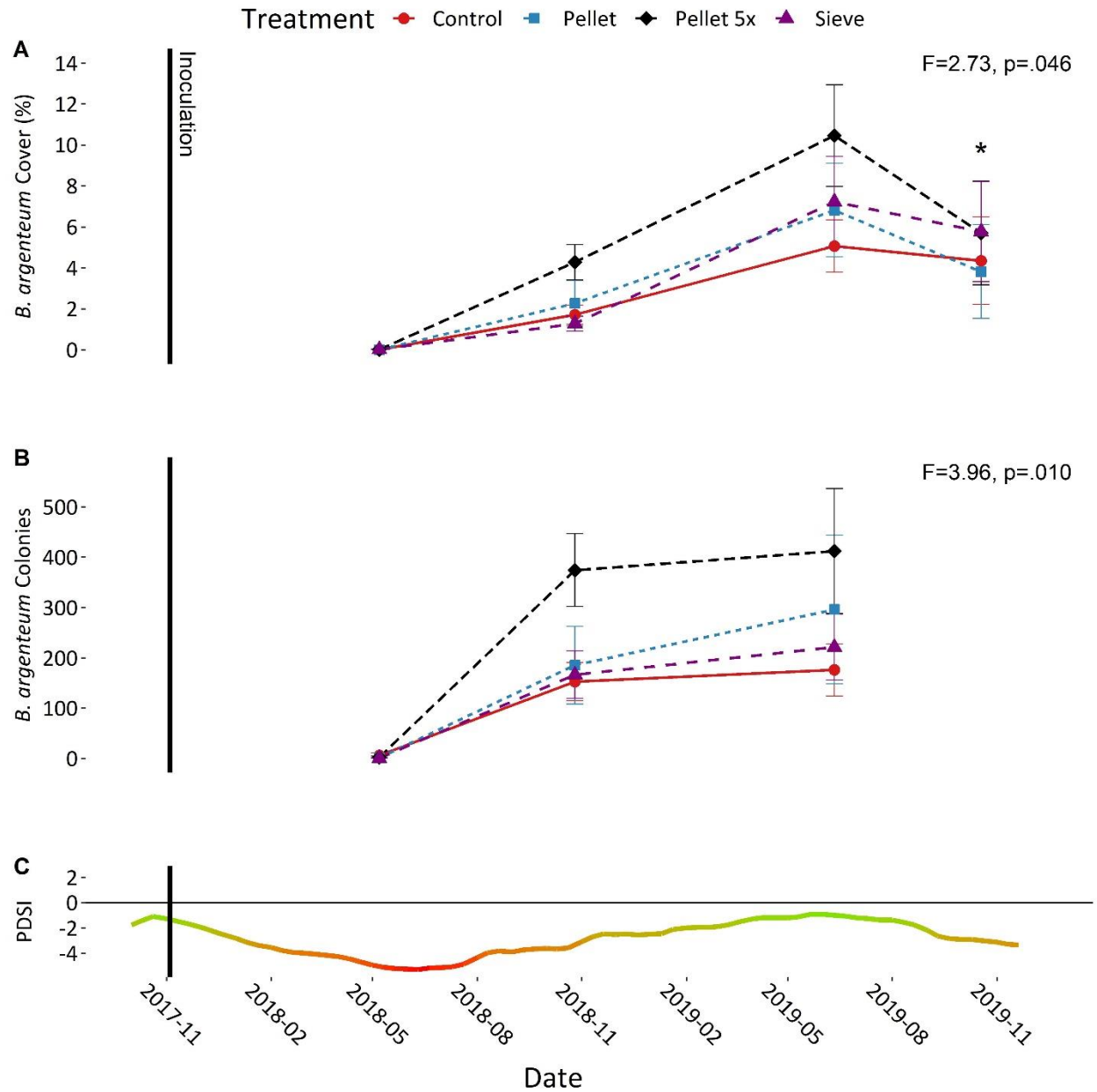


Figure 4.4: Exp 3, vertical lines indicate date of inoculation. (A) *B. argenteum* cover and (B) colony count at monitoring visits. *Cover methodology changed, and no colony count data was taken in final monitoring visit due to extensive vascular plant colonization. (C) Palmer drought severity index (PDSI) throughout the experiment, negative values indicate drought while positive indicate moisture. Error bars represent \pm SE.

Table 4.1: Soil properties for Exp. 2 and 3 at inoculation July 2017 and November 2017 respectively.

Fire	Exp.	pH	C (%)	N (%)	P (ppm)	Ca (ppm)	Mg (ppm)	K (ppm)	Na (ppm)	S (ppm)	Al (ppm)	Mn (ppm)
Boundary	2	7.15	5.22	0.36	93	3190	332.7	719.9	83.7	59.6	12.6	31.4
Cajete	3	6.72	2.56	0.19	91	5098	654.3	1034	290.1	50	56.5	118.3

CHAPTER V

Fire Moss: a quickly colonizing community and potential tool for post-fire rehabilitation

In brief:

- Fire mosses colonize conifer forests in the southwestern US after severe wildfires
- They achieve the highest cover on shady slopes two years after fire that were wet mixed-conifer forests before the fire.
- Fire moss covered soils resist erosion and increase infiltration when compared to bare soils.
- Fire moss can be grown in the greenhouse quickly, with times to harvest of ~2 months. This is achieved using an organic substrate, constant hydration via wicking from below, and a shade cloth to increase humidity.
- Field trials of greenhouse grown fire moss in recently burned areas had partial success. Pelletization of moss and diatomaceous earth decreased moss predation by ants and allowed for establishment however cover remained low due to drought.

Fire moss natural colonization and contribution to ecosystem function

Fire mosses consist of three species of early successional bryophytes, *Ceratodon purpureus* (Redshank), *Funaria hygrometrica* (Cord moss), and *Bryum argenteum* (Silvergreen moss), that can quickly recolonize after high severity wildfire in the southwestern US (**Fig 5.1**). Fire mosses have global distributions and can be found in many ecosystem types, but in the western US, high cover occurs primarily in severely burned forests. We conducted a survey of post-fire moss colonization near Flagstaff and the White Mountains of Arizona, and in the Jemez Mountains of New Mexico. This survey was restricted to patches of high canopy burn severity and ponderosa

to wet mixed-conifer forest types. Moss cover was highest two years postfire, but this result is not conclusive as we were unable to test a wide range of forest types one-year postfire. By seven years postfire moss cover had decreased, likely due to competition from vascular plants. Moss cover was highest on shady north facing slopes that had been wet mixed conifer forests pre-fire. Mosses were less abundant on south facing slopes that receive more sunlight, and locations where pre-fire organic carbon was low such as dry mixed conifer and ponderosa pine forests. During this survey, we tested for moss-associated changes in function and found a >100% increase in erosion resistance metrics and >50% increase in infiltration when compared to bare soil (**Fig. 5.2**). These results suggest that managers should monitor and try to promote moss cover on burned hillslopes and avoid disturbances that could inhibit its growth after fire.

Fire moss can be grown quickly in the greenhouse

One way to increase the rate of moss colonization post-fire is by growing and adding vegetative propagules in the form of gametophyte fragments. To achieve this goal, we focused on greenhouse cultivation of fire moss allowing us control over atmospheric, edaphic, and hydrologic conditions. We found that fire moss achieved high cover in two months when 2mm fragments were sprinkled on commercially available [garden soil](#) with constant wicking hydration provided by rockwool hydroponic slabs and a protective shade covering, but growth was not favored by addition of burned materials (**Fig. 5.2**). To grow enough moss for field trials, this technique was deployed on 120 x 55 cm trays and rotation times were shortened by adding weed cloth below the substrate so mosses could be removed and dried slowly separately at the end of each growth period. Slow drying is necessary to prevent tissue damage.

Fire moss can be established on severely burned soils, but cover remains low

In this study we tested the effectiveness of adding moss fragments to recently severely burned soils. We conducted three sequential experiments using knowledge gained from previous experiments to fine tune fire moss delivery methods. Study site locations were largely dictated by availability of recently severely burned soils but results from the natural survey were used to verify that moss restoration was feasible. Directly after a fire, we added moss tissue passed through a 2mm sieve, which was immediately collected by ants. In a second experiment, we added sieved moss alongside moss rolled into pellets using diatomaceous earth. Pellets were made by placing 250 ml of sieved moss into a 5-gallon bucket with 250ml of diatomaceous earth. A pump sprayer was used to shoot a jet of water into the bucket while it was being twisted back and forth to roll everything up into pellets. Pelletization increased *B. argenteum* establishment, but cover remained low (~1%) throughout monitoring which concluded 2 years after inoculation. The third experiment was started 4 months after a fire in the Jemez mountains. Pelletized moss, and pelletized moss at 5× application rate was added to a burned forest. 5× pelletized moss increased cover to 10% after 1.5 years; however, treatments largely converged afterward. At both study sites, an exceptional drought during the winter of 2017/2018 occurred which likely dampened our success. Researchers have recently developed a low-cost bicycle powered [pelletization machine](#) which could be helpful in scaling up future restoration trials. We believe that pelletization was an effective deterrent to ant herbivory with added benefits of attaching moss propagules to the soil surface and could assist in mechanized delivery of moss fragments. The partial success of these trials creates a framework for future research. However, we do not yet suggest this as a viable postfire rehabilitation technique.

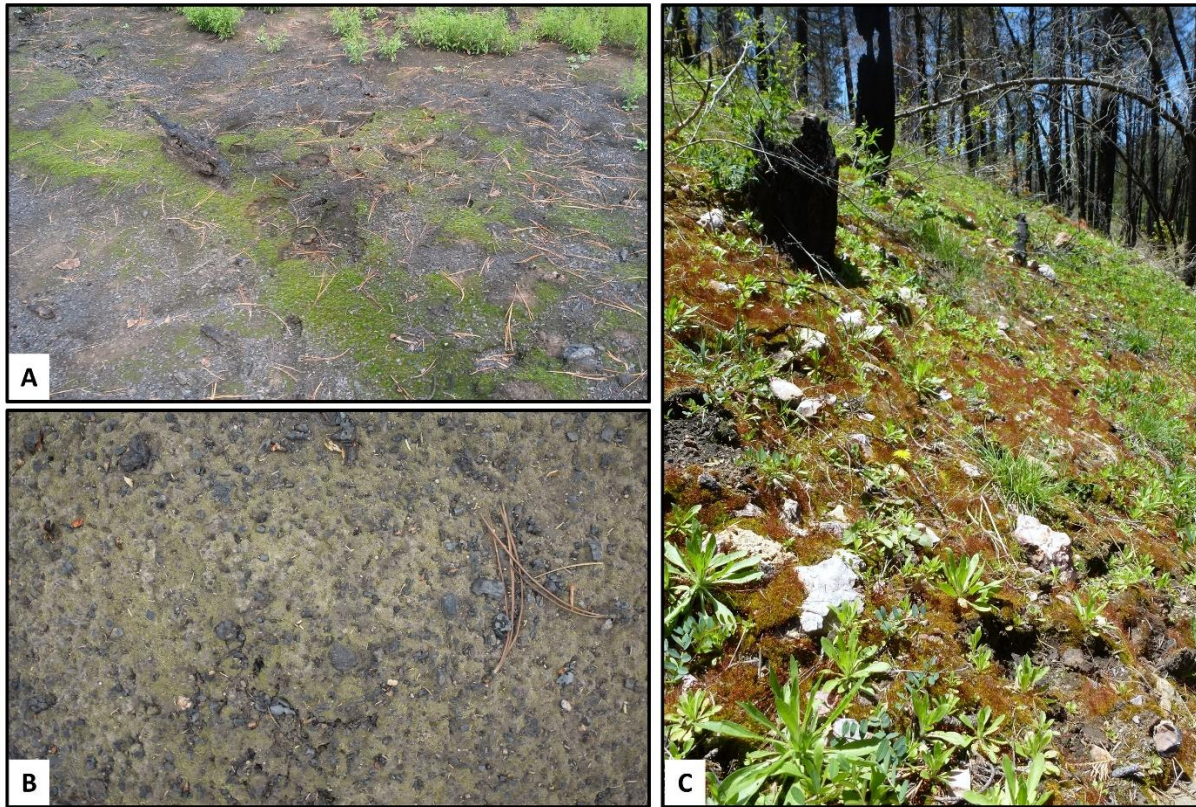


Figure 5.1: Fire moss four months after (A) the Boundary Fire, AZ with *F. hygrometrica* dominating, (B) the Cajete Fire, NM with *B. argenteum* dominating, and (C) two years after the Slide fire with *C. purpureus* dominating.

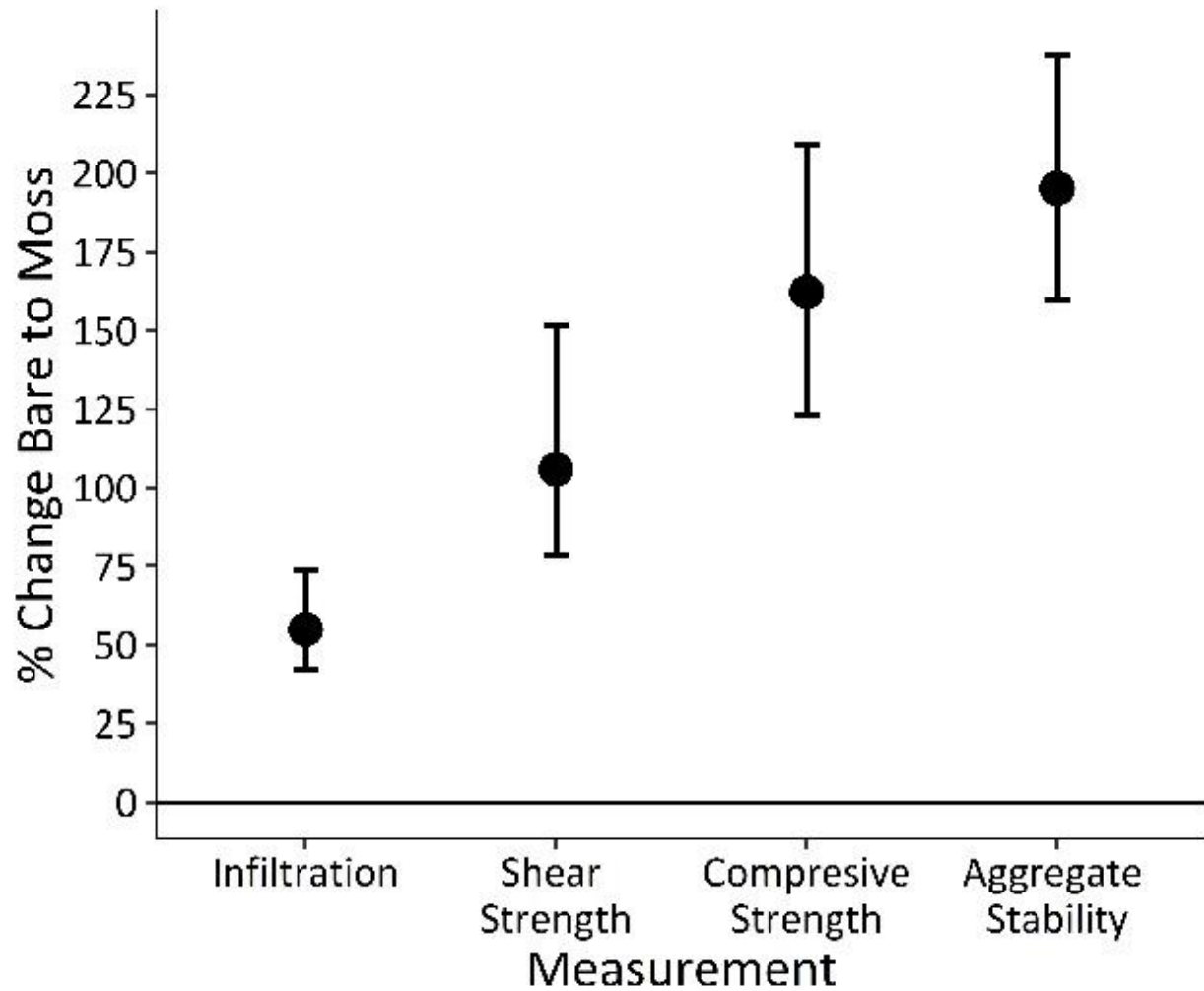


Figure 5.2: Percent change in hydrologic function (infiltration) and erosion resistance (shear strength, compressive strength, aggregate stability) from bare to moss-covered microsites. Error bars are bootstrapped 95% confidence intervals.

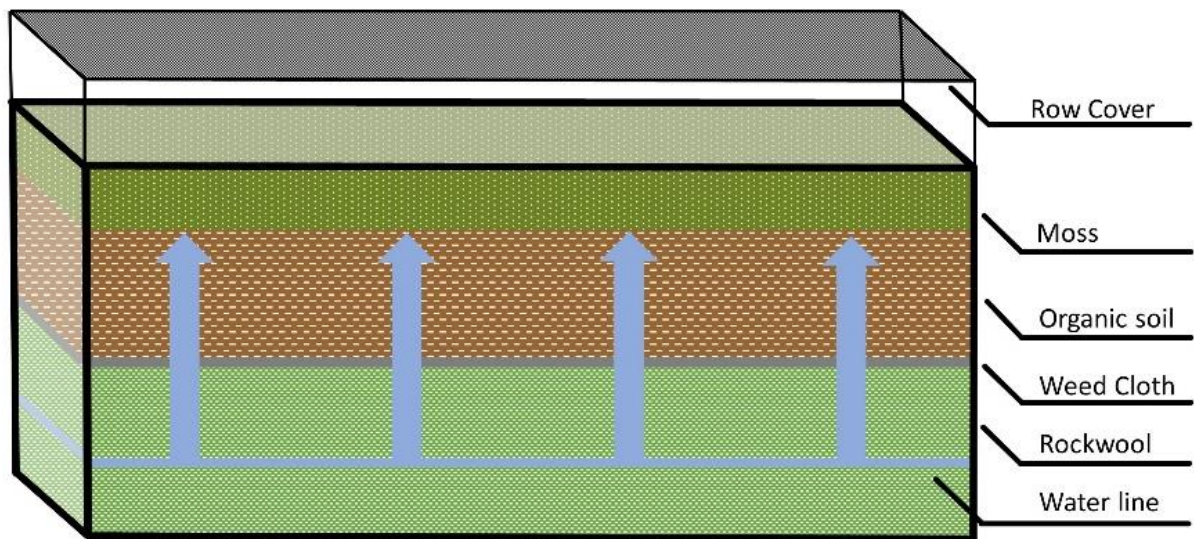


Figure 5.3: Water is ponded in bottoms of basin and wicks from below to keep mosses fully hydrated throughout cultivation. All equipment can be reused in successive cultivation runs.